

SOCIAL INSECTS IN THE TROPICS

Pierre JAISSON
Editor

Volume 1

SOCIAL INSECTS IN THE TROPICS

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International Organizing Committee : José L. Carrillo (President of S.M.E.), Charles D. Michener (President of IUSSI), Dieter Enkerlin (Mexico), Philip E. Howse (U.K.), Pierre Jaisson (France), Raul Ondarza (Mexico)

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LIST OF PARTICIPANTS

R.H. BEAL *Southern Forest Experiment Station, Forest Service, USDA, Gulfport, MS, U.S.A.*

A.P. BHATKAR *Department of Entomology & Nematology, University of Florida, Gainesville, Fl., U.S.A., and Depto. Entomologia, CSAT, Cardenas, Tab., Mexico.*

R.D. BUXTON *Istituto di Ecologia, Universita di Parma, Parma. Italy.*

A. CARDENAS F. *Division de Graduados en Agricultura, ITESM, Monterrey, N.L., Mexico.*

J.M. CHERRETT *Dept of Applied Zoology, University College of North Wales, Bangor, Gwynedd, U.K.*

H. COLES *Chemical Entomology Unit. University of Southampton, U.K.*

I. CUADRIELLO A. *Instituto de Biología, UNAM, Mexico D.F., Mexico.*

R. DARCHEN *Station Biologique, Université P. et M. Curie, Les Eyzies, France.*

A. DE HARO V. *Depto. de Zoología, Universidad Autónoma de Barcelona, Bellaterra, España.*

A. DEJEAN *Laboratoire de Biologie des Insectes, Université Paul-Sabatier, Toulouse, France.*

B. DELAGE-DARCHEN *Station Biologique, Université P. & M. Curie, Les Eyzies, France.*

M.A. & M.W. DIX *Universidad del Valle de Guatemala, Guatemala City, Guatemala, C.A.*

W. ENGELS *Institut für Biologie III, Universität Tübingen, Tübingen, Germany.*

D. ENKERLIN S. *División de Graduados en Agricultura, ITESM, Monterrey, N.L., Mexico.*

H.G. FOWLER *Department of Entomology & Economic Zoology, Rutgers University, New Brunswick, N.J., U.S.A.*

J.B. FREE *Rothamsted Experimental Station, Harpenden, Herfordshire, U.K.*

D. FRESNEAU *Laboratoire d'Ethologie et Sociobiologie, Equipe de Recherche Associée au C.N.R.S., n° 885, Université Paris XIII, Villetaneuse, France.*

J. GARCIA PEREZ *Centro de Investigaciones Ecologicas del Sureste, Tapachula, Chis., Mexico.*

L.S. GONÇALVES *Departemento de Genética, Universidade de Sao Paulo, Ribeirão Preto, São Paulo, Brazil.*

G. HALFFTER *Instituto de Ecología, Mexico D.F., Mexico.*

W.D. HAMILTON *Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.*

M.J.A. HEBLING-BERALDO *Departamento de Zoologia, Instituto de Biociencias, UNESP, Rio Claro, Sao Paulo, Brazil.*

P.E. HOWSE *Chemical Entomology Unit. University of Southampton, U.K.*

S.P. HUBBELL *Department of Zoology and Department of Chemistry, The University of Iowa, Iowa City, Iowa, U.S.A.*

J.H. HUNT *Dept of Biology, Univ. of Missouri, St. Louis, MO., U.S.A.*

J. IPINZA REGLA *Facultad de Ciencias Veterinarias, Universidad de Chile, Santiago, Chile.*

K.W. JAFFE C. *Depto. de Etudios Ambientales, Universidad Simon Bolivar, Caracas, Venezuela.*

P. JAISSON *Laboratoire d'Ethologie et Sociobiologie, Equipe de Recherche Associée au C.N.R.S., n° 885, Université Paris XIII, Villetaneuse, France.*

L.K. JOHNSON *Department of Zoology, University of Iowa, Iowa City, Iowa, U.S.A.*

B. KRAFFT *Laboratoire de Biologie du Comportement, Université de Nancy I, Nancy, France.*

A. LENOIR *Equipe de Recherche Associée au C.N.R.S. n° 885, Université Paris XIII, Villetaneuse, France.*

M.G. LEPAGE *Laboratoire de Zoologie, Ecole Normale Supérieure, Paris, France.*

V.L. LETIZIO MACHADO *Departamento de Zoologia, Instituto de Biociencias, Universidad Estadual Paulista «Julio de Mesquita Filho», Campus de Rio Claro, S.P., Brazil.*

R. LEUTHOLD *Abteilung für Zoophysiologie, Universität Bern, Bern, Switzerland.*

J. LEVIEUX *Laboratoire d'Ecologie Animale, Université d'Orléans, Orléans, France.*

R. MACGREGOR L. *Instituto de Biología, UNAM, México D.F., México.*

R.W. MATTHEWS *Department of Entomology, Univ. of Georgia, Athens, GA, U.S.A.*

J.K. MAULDIN *Southern Forest Experiment Station, Forest Service, USDA, Gulfport, MS, U.S.A.*

C.D. MICHENER *Department of Entomology, University of Kansas, Lawrence Kansas, U.S.A.*

S.B. NOGUEIRA *Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, M.G., Brazil.*

J.A. NÚÑEZ *Fisiología del Comportamiento, Centro de Biofísica y Bioquímica, Inst. Venezolano de Investigaciones Científicas, Caracas, Venezuela.*

G.W. OTIS *Department of Systematics and Ecology, University of Kansas, Lawrence Kansas, U.S.A.*

L. PASSERA *Laboratoire de Biologie des Insectes, Laboratoire associé au CN.R.S. n° 333, Université Paul-Sabatier, Toulouse, France.*

J.V. PEREZ MORALES *Centre for Overseas Pest Research, College House, Wrights Lane, London, U.K.*

G.D. PRESTWICH *Dept. of Chemistry, State Univ. of New York, Stony Brook, N.Y., U.S.A.*

J. RAMOS E. DE CONCONI *Instituto de Biología, UNAM, México D.F., México.*

C.W. RETTENMEYER *University of Connecticut, Storrs, CT, U.S.A.*

P. REYES CASTILLO *Instituto de Ecología, México D.F., México.*

T.E. RINDERER *Bee Breeding and Stock Center Lab., USDA, Baton Rouge, Louisiana, U.S.A.*

D.W. ROUBIK *Smithsonian Tropical Research Institute, Balboa, Panama, C.A.*

G. SAMPEDRO R. *Instituto de Biología, UNAM, México D.F., Mexico.*

J. & L. SCHUSTER *Depto. de Biología, Univ. del Valle de Guatemala, Guatemala, C.A.*

R. SYLVESTER BRADLEY *Instituto Nacional de Pesquisas de Amazonia, Manaus, Amazonas, Brazil.*

O.R. TAYLOR *Department of Entomology, University of Kansas, Lawrence, Kansas, U.S.A.*

B.L. THORNE *Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A., and Smithsonian Tropical Research Institute, Balboa, Panama.*

J. VALENZUELA G. *Centro de Investigaciones Ecológicas del Sureste, Tapachula, Chis., Mexico.*

M.J. WEST-EBERHARD *Smithsonian Tropical Research Institute, Balboa, Panama and Escuela de Biologia, Universidad de Costa Rica, Costa Rica, C.A.*

R.M.C. WILLIAMS *Centre for Overseas Pest Research, College House, Wrights Lane, London, U.K.*

M.L. WINSTON *Simon Fraser University, Vancouver, B.C., Canada.*

J.A. ZOZAYA R. *Dirección General de Avicultura y Especies Menores, SARH, México D.F., Mexico.*

SOCIAL INSECTS IN THE TROPICS

VOLUME I

PREFACE

During the last Congress of the International Union for the Study of Social Insects (I.U.S.S.I.), which took place in Wageningen (Holland) in 1977, it was suggested that the next international meeting organized by the Union should take place in a Third-World country and should cover topics more directly related to tropical regions.

The first international symposium «Social Insects in the Tropics» the Proceedings of which are published in these volumes, is the result of that suggestion. This was also the first international meeting on Social Insects to take place in the Western Hemisphere. It required two years of preparation from the time it seemed to me that Mexico was one of the most appropriate countries in which to hold this meeting, and the collaboration of many individuals and scientific and cultural organizations to bring this idea to fruition.

From the outset, the encouragement of Dr. Raúl N. Ondarza, Secretary general of the committees of the Consejo Nacional de Ciencia y Tecnología (CONACYT), and Dr. Gonzalo Halffter, Director of the Instituto de Ecologia of Mexico city, convinced me that there was a real possibility of organizing this symposium in Mexico. The interest and support of the project by Dr. Edmundo Flores, Director general of the CONACYT, permited the speedy constitution of International and Local Organizing committees, the latter of which was formed from the Board of Directors of the Sociedad Mexicana da Entomología. The President of this Society, Dr. José-Luis Carrillo, played a critical role in the local committee's coordination. He also partipated in the scientific work of the international organizing committee with Drs. R.N. Ondarza and Enkerlin (Mexico), and Professors C.D. Michener, President of I.U.S.S.I. (U.S.A.), and P.E. Howse, Secretary general of I.U.S.S.I. (Great Britain) who gave his support to the project from the start. The active support of all these individuals was determinant for the success of the symposium.

Nothing would however have been possible without the material support of various national and international institutions. The CONACYT was particularly helpful and we would like to thank this organization on behalf of the scientific community. Other institutions we would like to thank are the Universidad Nacional Autónoma and the Instituto Politécnico

Nacional of Mexico, the Instituto Nacional de Investigaciones Agrícolas and the Colegio de Postgraduados en Agricultura who organized an international training course on social insects.

We are grateful for the collaboration of the Instituto de Ecología, the Centro de Investigaciones Ecológicas del Sureste (CIES) and the Instituto Nacional de Investigaciones Sobre Recursos Bióticos, and also of UNESCO who provided some assistance.

The cooperation by these different organizations helped to make possible the publication of the Proceedings of the symposium, as was the collaboration and effort of the 5th Circonscription of the French Centre National de la Recherche Scientifique and the Université Paris XIII.

It is obviously impossible by this means to faithfully reproduce the richness of the discussions between the researchers of 14 different countries. However, we hope that these two volumes, with their 34 contributions, divided according to general topics or by species (as for the round table organized by Professor Michener on the africanized Honeybee), will constitute a basic reference source for present and future investigators of tropical social insects. This is the first specialized international work on this topic. It was produced without any commercial motivation, which permited the reduced sale-price. The financial proceeds will be used for the purpose of organizing other new scientific meetings.

Finally, we are particularly grateful for the cooperation of the 51 specialists, authors of the works that are included in these volumes.

February, 15th, 1982

Pierre Jaisson
Professor at the University Paris XIII
President of the French Section of
I.U.S.S.I.

PRÉFACE

Lors du dernier congrès de l'Union Internationale pour l'Etude des Insectes Sociaux (U.I.E.I.S.) qui s'est tenu en 1977 à Wageningen (Pays-Bas), fut exprimé le souhait qu'une prochaine manifestation internationale, organisée sous l'égide de l'Union, puisse se tenir dans un pays du Tiers-Monde et sur des problèmes intéressant plus directement les zones tropicales.

Le premier symposium international «Insectes Sociaux sous les Tropiques» – dont les comptes rendus sont rassemblés dans cet ouvrage – est la matérialisation de cette volonté. C'est également le premier colloque international sur les sociétés d'insectes à se tenir dans le nouveau monde. Deux années d'efforts ainsi que le concours de nombreuses personnalités et organisations scientifiques ou culturelles furent nécessaires pour aboutir à ce résultat, à partir du moment où il m'avait semblé que le Mexique était l'un des pays les mieux placés pour accueillir cette manifestation.

Dès le début du projet les encouragements du Docteur Raúl N. Ondarza, Secrétaire général des Comités du Consejo Nacional de Ciencia y Tecnología (CONACYT), et du Docteur Gonzalo Halffter, Directeur de l'Instituto de Ecología de Mexico, m'ont démontré que la possibilité existait effectivement d'organiser cette réunion scientifique au Mexique. L'intérêt et l'appui du Docteur Edmundo Flores, Directeur général du CONACYT, permirent d'aboutir rapidement à la constitution d'un Comité International et d'un Comité Local d'Organisation issu du Conseil de Direction de la Société Mexicaine d'Entomologie. L'action du Docteur José-Luis Carrillo, Président de cette Société, fut déterminante au niveau de la coordination du Comité local. Il participa également aux travaux du Comité International avec les Docteurs R.N. Ondarza et D. Enkerlin (Mexique), les Professeurs C.D. Michener, Président de l'U.I.E.I.S. (Etats-Unis) et P.E. Howse, Secrétaire général de l'U.I.E.I.S. (Royaume-Uni) lequel, dès le départ, apporta son soutien au projet. Toutes ces personnalités qui ont donné leur concours actif, sont responsables de la réussite du symposium.

Mais rien n'aurait été possible sans le soutien matériel d'institutions nationales ou internationales. En particulier, l'appui du CONACYT a été déterminant et nous lui témoignons ici notre reconnaissance au nom de la communauté scientifique, de même qu'à l'Universidad Nacional Autónoma

et à l'Instituto Politécnico Nacional du Mexique, à l'Instituto Nacional de Investigaciones Agrícolas et au Colegio de Post-graduados en Agricultura, lequel organisa à cette occasion un cours international sur les insectes sociaux.

Nous remercions également l'appui de l'Instituto de Ecología, du Centro de Investigaciones Ecológicas del Sureste (CIES) et de l'Instituto Nacional de Investigaciones sobre Recursos Bióticos, ainsi que l'UNESCO, qui nous apporta son aide.

C'est grâce à ces différents concours qu'a pu être envisagée l'édition des comptes rendus du symposium, mais également grâce à la collaboration du Centre National de la Recherche Scientifique (5ème Circonscription) et de l'Université Paris XIII.

Il est évidemment impossible de traduire, dans toute leur richesse, sous la forme d'un tel ouvrage, les discussions qui se sont déroulées entre les chercheurs de 14 pays différents. Cependant nous espérons que ces deux volumes, qui rassemblent 34 contributions réparties par thèmes généraux ou par thèmes d'espèces (cas de la table ronde sur l'Abeille africanisée, organisée par le Professeur Michener) constituent une référence pour les chercheurs actuels et à venir intéressés par les insectes sociaux tropicaux. Il s'agit du premier ouvrage spécialisé de niveau international existant sur ce thème. Il a été réalisé sans aucun but lucratif, ce qui a permis de déterminer un prix de vente particulièrement intéressant. Les produits de la vente serviront à l'organisation d'autres réunions scientifiques.

Je terminerai cette préface en remerciant tout particulièrement de leur concours les 51 spécialistes auteurs des articles contenus dans cette édition.

Le 15 février 1982

Pierre Jaisson
Professeur à l'Université Paris XIII
Président de la Section française
de l'U.I.E.I.S.

PREFACIO

Durante el último congreso de la Unión Internacional para el Estudio de los Insectos Sociales (U.I.E.I.S.), que tuvo lugar en Wageningen (Holanda) en 1977, se manifestó el deseo de que la Unión organizará la siguiente reunión internacional en un pais del Tercer Mundo y tratando sobre problemas que interesan más directamente a las zonas tropicales.

El primer simposio internacional «Los Insectos Sociales en el Trópico», cuyas actas estan reunidas en esta obra, fué la materialización de este deseo, fué también el primer coloquio internacional de esta especialidad que se efectua en el nuevo mundo. Pero fueron necesarios dos años de esfuerzos y la participación de numerosas personalidades y organizaciones científicas y culturales, para llegar a este resultado, à partir del momento en que me pareció que México era uno de los mejores lugares para acoger esta manifestación.

Desde el inicio del proyecto los estímulos del Dr. Raúl N. Ondarza, Secretario general de Comités del Consejo Nacional de Ciencia y Tecnologia (CONACYT) y del Dr. Gonzalo Halffter, Director del Instituto de Ecologia de México, me demostraron que existía efectivamente la posibilidad de organizar esta reunión científica en México. El interés y el apoyo del Dr. Edmundo Flores, Director general del CONACYT, permitieron lograr rapidemente la constitución de un Comité internacional y de un Comité local de Organización, habiendose originado este último de la Mesa Directiva de la Sociedad Mexicana de Entomologia (S.M.E.). La contribución del Dr. José Luis Carrillo, Presidente de la S.M.E., fué determinante como coordinador del Comité local, y también participó activamente en los trabajos realizados por el Comité internacional junto con los Drs. Raúl N. Ondarza y Dieter Enkerlin (México), los Professores Charles D. Michener, Presidente de la U.I.E.I.S. (E.U.) y Philip E. Howse, Secretario general de la U.I.E.I.S. (Inglaterra), quién desde el principio aportó su apoyo al proyecto. Todas estas personalidades tuvieron una participación activa, indispensable al éxito del simposio.

Pero nada de esto habría sido posible sin el apoyo material de Instituciones nacionales e internacionales. El apoyo del CONACYT fué determinante, por lo cual le manifestamos aqui el reconocimiento de la comunidad

científica, así como a la Universidad Nacional Autónoma de México, al Instituto Politécnico Nacional, al Instituto Nacional de Investigaciones Agrícolas y al Colegio de Postgraduados de Chapingo, el cual organizó en esta ocasión un curso internacional sobre insectos sociales.

Agradecemos también el apoyo del Instituto de Ecología, del Centro de Investigaciones Ecológicas del Sureste y del Instituto Nacional de Investigaciones sobre Recursos Bióticos, así como a la UNESCO por la ayuda que nos aportó.

Fué gracias a todas esta instituciones que ha sido posible realizar la edición de las Actas del Simposio, y también gracias a la colaboración del Centre National de la Recherche Scientifique (5e circonscription) y de la Université Paris XIII.

Obviamente es imposible traducir bajo esta forma toda la riqueza de las discusiones que se desarrollaron entre investigadores de 14 paises diferentes. Sin embargo, esperamos que estos dos volúmenes, que reunen 34 contribuciones repartidas por temas generales o por temas de especies (como en el caso de la mesa redonda organizada por el Professor Michener sobre la abeja africanizada), constituyan una referencia para los investigadores actuales y futuros interesados en los insectos sociales tropicales. Esta es la primera obra especializada, de carácter internacional, existente sobre el tema. Fué realizada sin ninguna finalidad lucrativa, lo que permitió fijar un precio de venta particularmente interesante. Los productos de la venta servirán para organizar otras reuniones científicas.

Terminaré este prefacio agradeciendo muy particularmente a los 51 especialistas, autores de los artículos incluidos en esta edición.

15 de febrero de 1982

Pierre Jaisson
Profesor de la Universidad de Paris XIII
Presidente de la Seccion francesa de la
U.I.E.I.S.

CASTE DETERMINISM

REPRODUCTIVE PLASTICITY IN THE NEOTROPICAL TERMITE *NASUTITERMES CORNIGER*

B.L. THORNE

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 U.S.A.

and

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

SUMMARY

Colonies of the arboreal Neotropical termite *Nasutitermes corniger* display an exceptionally diverse combination of reproductive patterns. Colonies can be monogynous or polygynous. Independent alates can initiate nests, or daughter colony «buds» can split from a parent nest. A dead queen or king is replaced either by alates within the nest, or by ergatoid reproductives developed from workers. This degree of intraspecific plasticity is a new finding among the Termitidae, and such marked flexibility is rare among the eusocial insects as a whole.

RESUMEN

Plasticidad reproductiva en la termita neotropical *Nasutitermes corniger*

Las colonias de termitas arboreas neotropicales *Nasutitermes corniger*, despliegan una combinación exceptionalmente diversa de patrones reproductivos. Las colonias pueden ser monogénicas o poligénicas. Aladas independientes pueden iniciar nidos, o los jóvenes de la colonia hija pueden dispersarse del nido de sus padres. Una reina o un rey muerto



Fig. 1 – Nine primary queens and four primary males found in a *Nasutitermes corniger* colony collected May 22, 1980 in Frijoles, Republic of Panama.

Fig. 1 – Nueve reinas primarias y cuatro machos primarios encontrados en una colonia de *Nasutitermes corniger* colectada el 22 de mayo de 1980 en Frijoles, República de Panama.

pueden ser remplazados ya sea por alados dentro del nido o por suplementos (ergatoid) reproductivos desarrollados a partir de obreras. Este grado de plasticidad intraespecífica es nuevo desenvolvimiento dentro de los *termitidea* y esta marcada flexibilidad es rara dentro de los insectos eusociales como un todo.

Eusocial insects exhibit a diverse array of reproductive patterns. Colonies can be founded by one or more reproductives (*independent founding*) or by reproductives joined by a group of sterile workers (*budding* or *swarming*). Some mature colonies have a single queen (*monogyny*), others have two or more fecund queens concurrently (*polygyny*). The number of queens may change over the life cycle of the colony (Hölldobler & Wilson, 1977 ;

Oster & Wilson, 1978 ; West-Eberhard, 1978a, b). If the queen dies, she may be replaced by a young reproductive, or members of the worker caste may develop functional ovaries and become egg layers. Despite the plasticity across the eusocial insects as a whole, the reproductive organization within any single species of ant, bee, wasp or termite is usually restricted. Frequently there is no intraspecific flexibility in mode of colony foundation : species with independent founders may not be capable of swarming, and vice versa (Evans & West-Eberhard, 1970 ; Spradbery, 1973 ; Hölldobler & Wilson, 1977 ; West-Eberhard, 1978b). Many species are obligately monogynous (Hölldobler & Wilson, 1977 ; West-Eberhard, 1978b). Queen replacement is often solely via young reproductives because workers in a number of species are irreversibly sterile (Wilson, 1971).

This paper describes the first case of a higher termite with intraspecific expression of the entire diversity of principal reproductive options. Colonies of the Neotropical termite *Nasutitermes corniger* (Motschulsky) studied in second growth areas of the Republic of Panama (Frijoles and the Gigante Peninsula, former Canal Zone) are sometimes founded by mating pairs and sometimes by buds from a parent nest. Reproductively mature colonies have from 1-22 fully physogastric primary queens, and occasionally more than one king (Dudley & Beaumont, 1889a, b, 1890 ; Dietz & Snyder, 1923 ; Thorne, 1982)[1] (see Figure 1). Available data suggest that in polygynous colonies the number of queens is reduced over time. Colonies can be re-queened or re-kinged with young reproductives, or less frequently, ergatoid (third-form) reproductives develop from workers (Thorne & Noirot, 1982). These broad alternatives in reproductive method and organization give *N. corniger* a marked ecological flexibility (see Figure 2).

The ellipsoidal nests of *Nasutitermes corniger* are constructed of a network of carton galleries surrounding a very dense queen cell. Large workers, small workers and nasute soldiers compose the non-reproductive «neuter» castes. A large *N. corniger* nest harbors a neuter population of from 500,000 - 800,000 individuals[2]. Alates, the fertile winged reproductives, are produced once a year and fly during the early rains of the wet season (April - June) (Dudley & Beaumont, 1889b ; Dietz & Snyder, 1923 ; personal observation). Independent founding is the most common mode of colony foundation in *N. corniger*. Alates fly from the parent nest, land to find a mate, drop their wings and depart to search for a nest site where they will start new colonies. Alternatively, new *N. corniger* colonies can be formed by budding, a process described only rarely in the order Isoptera (reviewed in Nutting, 1969). In four cases, mature *N. corniger* colonies were observed to form daughter «satellite» nests located within 2 m of the original nest, and initially connected by covered trails to the parent colony. The young satellite nests expanded

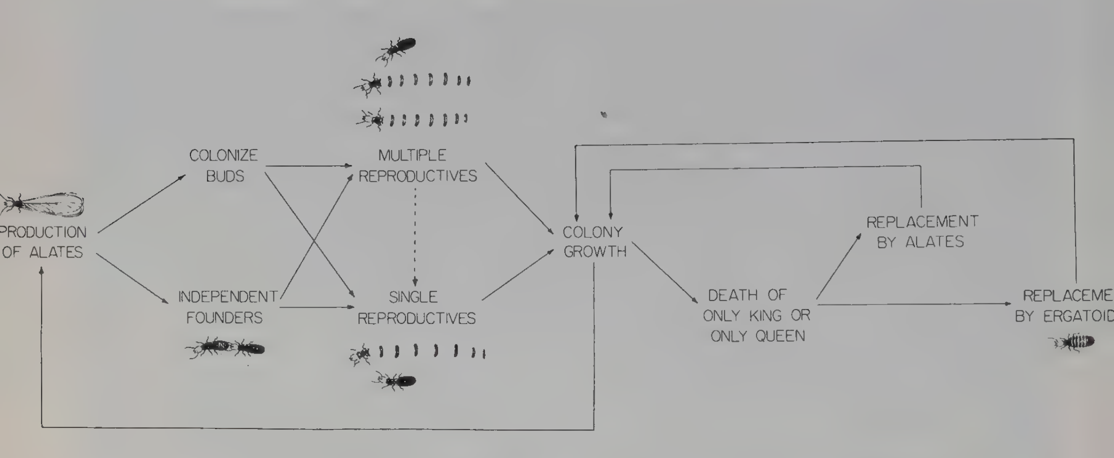


Fig. 2 —Life history flexibility in *Nasutitermes corniger.* Not all pathways are followed with equal frequency. The number of queens in polygynous colonies may decrease as individual queens grow larger, but that transition line is tentative (dashed) because there is only circumstantial evidence of its occurrence.

Fig. 2 — Flexibilidad de la historia natural de *Nasutitermes corniger.* No todas las secuencias son seguidas con la misma frecuencia. El número de reinas en las colonias polígınas puede decrecer pero en este caso son individualmente más voluminosas ; la línea de transición es tentativa (discontinua) porque solamente hay evidencias circumstanciales de su ocurrencia.

rapidly, the population growth being accelerated by immigration of neuters from the original nest[3]. Alates were produced in three of the parent colonies[4]. One or more alates of each sex did not fly, and instead moved into the new nest bud, apparently to assume reproductive status[5]. In a separate case, an *N. corniger* colony of unknown history was collected six weeks after the alate flights in 1979. It was full of mature soldiers and workers, but had no eggs, no immatures, and five young de-winged alates (three females ; two males). The nest was small and constructed of thin carton. That colony was probably a bud as well.

Independent founders can disperse to distances far from the parent nest. As a consequence, they do not draw away energetically costly mature neuters from their mother's colony. Alates joining buds begin their colonies with a pre-existing neuter support staff capable of getting food, defending and expanding the nest, and caring for new brood. For these reasons, the growth rate and probability of survival of the buds may be significantly higher than in colonies of the same age founded by independent alates.

Formation of satellite buds in *N. corniger* is ecologically distinct from «accidental» fracture of a colony and subsequent maturation of neotenics in the queenless portion, a process occurring in a number of termite species (reviewed in Nutting, 1969). *N. corniger* budding is an active, deliberate division (similar to the «sociotomy» reported in *Anoplotermes* sp. and *Trinervitermes bettoniamus* Sjöstedt by Grassé and Noirot, 1951). The reproductives which head the newly budded *N. corniger* nests are dewinged alates (primary reproductives).

Most termite species are reported to be exclusively monogynous and monoandrous : colonies have a single pair of primary reproductives, the queen and the king. Of 69 dissected *Nasutitermes corniger* nests with *at least one* queen, 21 colonies had *multiple* primary queens, and two had multiple primary kings[6]. Polygyny involving primary queens has been documented only rarely among the Isoptera (reviewed in Thorne, 1982), and never in the relatively high frequency found in *N. corniger*. Reproductives in each *N. corniger* colony were always found in the same queen cell, either all in the same chamber or divided among adjoining chambers. Each queen in a polygynous association is a functional egg-layer. Mature (alate producing) colonies can be polygynous. No signs of aggression have been observed between queens from a single colony, although laboratory observation conditions are not comparable to the nest environment. Monogyny is not found exclusively in large colonies ; polygyny is not restricted to small colonies.

The maximum wet weight recorded for a monogynous *N. corniger* queen was 0.5565 gms. The largest queen found in a polygynous nest weighed 0.3114 gms. In polygynous colonies with small queens (arbitrarily defined as $\leqslant 0.15$ gms), all females are of approximately the same size and weight. However, as the mean weight of queens within a polygynous group increases, so does the difference between their weights ($r = 0.676$; $p < .001$). When large numbers of queens are found in a single nest, all are usually small. Eight of the eleven polygynous colonies with a queen under 0.15 gms contained from 3-22 queens. Polygynous nests with larger queens tend to have fewer of them. Of the 10 polygynous colonies containing at least one queen weighing over 0.15 gms, only one had more than two queens. These data suggest that as individual queen size increases in polygynous colonies, the number of queens may be reduced[7].

The method of formation of polygynous *N. corniger* colonies, and thus the kin relationship among multiple reproductives, remains unclear. Available data imply that polygynous colonies can be initiated either by multiple independent founders or by a group of alates colonizing a bud. Three polygynous nests (containing 9, 10 and 18 queens respectively) were collected in Frijoles in April - June 1980. None of these nests were observed a year earlier in

an area I frequented constantly during the study. Each nest was isolated (> 150 m) from the nearest mature conspecific colony. All three nests were small to moderate in size ; none had dense carton construction (hard, heavily reinforced carton indicates an older nest). These colonies were probably initiated by a group of alate foundresses. Kin relationships among the queens are unknown. In the lab, alates from the same colony (sibs) or from different colonies will occupy lesions in wood (nesting sites) in groups of more than a single male-female pair. Successful colony initiation was never achieved in such experiments, but in one compartment in the center of a piece of wood I found 93 *N. corniger* alates (fungus growth present at the time of monitoring obscured genitalia and prevented a count of sex ratio). In a nest choice experiment involving only sibs, 20 male and 15 female alates were found in the same cavity. Because of the technical difficulties involved in following the ontogeny of a single colony over time without destructive sampling, precise tracking of polygynous associations is impossible. Nevertheless, it appears that colony foundation by a group of alates is possible as one route to polygyny. Buds seeded with more than one female alate may also form polygynous colonies. In such cases, all queens are definitely sibs, or half-sibs if the parent colony was itself polygynous (see Thorne 1982 for a related example in *N. ephratae*).

N. corniger colonies respond to king or queen death in one of several ways. If the neuter population size is small, the colony may not be able to replace a reproductive. Even if an alate egg or nymph is present, its development process takes several months. During that time colony health may be in jeopardy because no eggs are produced to replace the declining neuter population. If the king or queen dies when a mature colony has alates (or alate nymphs), it is probable that one or more of the alates will succeed the dead parent (such replacement reproductives are termed *adultoid* reproductives (Noirot, 1969)). Queen replacement by daughters has been documented in several species of Termitidae (reviewed in Noirot, 1969 ; Darlington, unpublished data). To unambiguously demonstrate this process, one must induce it experimentally (by queen removal : Coaton, 1949 ; Noirot, 1969 ; Darlington, unpublished data) or chance upon replacement in progress at the time of colony dissection.

I have circumstantial evidence for offspring replacement of parents (adultoid reproductives) in *N. corniger*. Of 29 colonies with at least one king, collected within six weeks of the major alate flights, seven (24.14 %) had from 2-13 de-winged males in or near the queen chamber. Four of these colonies were monogynous. The frequency of multiple males fell off sharphy in colonies dissected out of alate season (October - January). Of 31 nests with at least one king collected during that interval, only two (6.45 %) contained

multiple males. Both colonies also had small multiple queens. The marked increase in number of colonies with multiple male during alate season suggests that the additional males are temporary. Several male alates remain in the nest after the alate flights : eventually one will replace the old or dead king.

Several colonies seemed to be in the process of queen replacement at the time of dissection. Occasionally a relatively small queen is found in a large colony, or several de-winged female alates are found in a queenless colony. However, unambigous succession of a mother by her daughter in *N. corniger* must be demonstrated experimentally.

King replacement is expected to be more frequent than queen replacement. The wet weight of a mature king ($\bar{x}$ = .0102 gms., s = 0.0012, N = 31) is only slightly more than the wet weight of a male alate ($\bar{x}$ = 0.0097 gms.[8]). In contrast, the size of an *N. corniger* queen increases markedly from alate wet weight ($\bar{x}$ = 0.0121 gms.[8]) to size of maximum fecundity (largest queen wet weight found in this study = 0.5565 gms.). The time and energy investment in a physogastric queen is significant. When a large queen is replaced by a young alate, egg production drops dramatically (Thorne, 1982). The high rate of egg production will be restored only after a costly time lag accomodating the new queen's growth.

One queenless colony of *N. corniger* was collected on December 14, 1979 on the eastern side of Gigante peninsula while both large and small workers (approximately 770 individuals) were in the process of differentiating into ergatoid reproductives (large workers are females ; small workers are males). The remaining neuter population (estimated to include approximately 20,600 workers, soldiers and immatures) were phenotypically unchanged. Histological analysis (Thorne & Noirot, 1982) revealed that none of the ergatoids had reached maturity at the time of collection, although immature sexual organs were distinct. Ergatoid reproductives have been found only rarely in the Nasutitermitinae (Noirot, 1956). The environmental conditions inducing ergatoid formation in *N. corniger* are unknown, but it is significant that this developmental channel is open in this species.

DISCUSSION

The termite *Nasutitermes corniger* has an exceptionaly plastic intraspecific reproductive repertoire. Colony foundation can involve alates alone, or both alates and neuters in satellite buds from an established nest. Both monogyny and polygyny occur in this species. The number of queens in polygynous colonies appears to decrease as individual queens grow larger. Queens and kings can be replaced either by young alates or by ergatoid

(worker-derived) reproductives. Thus all major binary «either/or» gates for eusocial insect reproductive cycles are open in *N. corniger*. Some pathways are followed more frequently than others, but the developmental and ecological flexibility present in the system is remarkable. It is hypothesized that the exceptional plasticity of this phylogenetically advanced termite has enabled colonies to successfully adjust to variable microhabitats, disturbed conditions, and to recover from individual historical accidents.

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Footnotes

1 Primary (first-form) reproductives develop from mature alates. Second-form (brachypterous) reproductives common in some species of termite are unknown in *Nasutitermes corniger*.

2 These and other nest data given in this paper are based on complete dissections of entire *N. corniger* nests, excluding foragers outside the nest. Colonies were collected, sealed in large plastic bags, and refrigerated to induce torpor in the termites. Estimates of population size and caste composition were made from volumetric subsamples. Standard errors were consistently less than 10 % of the estimates.

3 Members of the parent and satellite nests do not fight when placed together. This compatability demonstrates that they are members of the same colony (reviewed in Thorne, 1982).

4 It is possible that the alate brood in the fourth parent colony was aborted after formation of the bud commenced. The satellite nest connected with that colony stopped expanding after a few months, and was relatively small at the time of dissection.

5 At the time of nest dissections none of the young reproductives in any of the buds had begun laying eggs, although many had shed their wings and were clustered around a crude queen cell (probably of recent construction). Since nest dissection is irreversibly destructive, it is impossible to follow the progress of the satellite colonies after sampling. All colonies were dissected after the peak alate flights of *N. corniger*, but apparently sexual maturation of alates inhabiting buds occurs well after that time.

Young alates of the closely related sympatric species *N. ephratae* did develop functional ovaries in a queenless colony composed of workers and soldiers (Thorne, 1982).

6 Colonies with multiple males considered to be in the process of king replacement are excluded from this count, and are discussed later in the paper.

7 Because no data exist on the relationship between queen size and age, it is difficult to obtain an exact description of this process. However, since egg production is proportional to queen weight (Thorne, 1982), selection will favor large queens (assuming that the ratio of alate : neuter eggs is constant or increasing with weight). The method of queen reduction is completely unknown.

8 Calculated as the mean of the average weight of alates from 10 colonies.

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DÉTERMINISME DES CASTES CHEZ MÉLIPONES ET TRIGONES

B. DELAGE-DARCHEN et R. DARCHEN

Université P. et M. Curie, Station Biologique,
24620 Les Eyzies, France

RÉSUMÉ

On effectue ici une revue des publications récentes concernant le déterminisme des castes chez les *Meliponini*, les *Trigonini* et *Apis mellifica.* L'analyse des différents travaux, y compris ceux des auteurs de ce travail, conduit à considérer que le déterminisme des castes chez toutes les Abeilles sans dard n'est pas fondamentalement différent de celui découvert chez *Apis mellifica.* Un contrôle trophogénique explique les résultats des expériences sur le déterminisme des castes beaucoup mieux que l'hypothèse génétique.

Finalement, ce travail conclut que la somme des informations sur le déterminisme des castes chez les Apidés est encore hétérogène et difficile à coordoner. Bien qu'on reconnaisse à la nourriture un rôle initiateur essentiel dans la détermination des castes, jusqu'ici, on attend encore le fin mot de l'explication.

SUMMARY

The trophic grounds of caste determination in Melipona **and** Trigona **(Hymenoptera, Apidae)**

Recent work is reviewed concerning caste determination in *Meliponini, Trigonini* and *Apis mellifica.* The analysis of different studies, including the author's own results leads them to consider that caste determination in the Stingless Bees is not fundamentally different to that found in other social bees, especially in *Apis mellifica.* A trophogenic

control explains the results of the experiments on the female caste better than the genetic hypothesis.

Finally, this work attempts to show that the amount of information on caste determination in *Apidae* is still relatively heterogenous and difficult to synthesize. Although the triggering role of diet in caste determination is now recognized by almost all specialists, the final explanation is still waiting.

INTRODUCTION

Une des caractéristiques des abeilles sans dard, trigones et mélipones est d'élever leur couvain dans des cellules approvisionnées une fois pour toutes avant la ponte de l'œuf et scellées ensuite jusqu'à l'éclosion de l'imago. Elles s'opposent en cela au genre *Apis* et même aux bourdons qui pratiquent une alimentation progressive des larves.

La nourriture larvaire des abeilles sans dard est constituée de régurgitations stomacales auxquelles s'ajoutent vraisemblablement des sécrétions salivaires. En effet, si l'on juge par analogie, on voit que les ouvrières de trigones et mélipones ont des glandes salivaires bien développées et en particulier, les glandes hypopharyngiennes, toutefois même si les présomptions sont fortes, aucune preuve réelle n'a été donnée jusqu'à présent d'un apport de salive à la préparation alimentaire distribuée au couvain.

La particularité des trigones est de posséder des cellules à couvain de taille différente selon qu'il s'agit de reine, de mâle ou d'ouvrière. Les cellules de reines, construites en assez petit nombre et, semble-t-il, suivant un rythme saisonnier sont nettement plus grandes que les autres. Quant aux cellules de mâle et d'ouvrières, elles sont nettement plus petites, mais indiscernables entre elles.

Les mélipones, au contraire, (et c'est là, la différence essentielle entre ces 2 groupes d'abeilles) construisent des cellules absolument identiques qu'il s'agisse de mâle, d'ouvrière ou de reine et lors des éclosions ces 3 catégories d'individus sont présents constamment. Dès leur apparition les reines, abondantes et inutiles sont chassées du nid par les ouvrières qui les expulsent de la ruche.

On sait depuis longtemps que chez *Apis mellifica*, les castes sont déterminées par la qualité de la nourriture distribuée aux larves par les ouvrières, la gelée royale, secrétée par les nourrices étant réservée aux larves destinées à devenir des reines. Mais qu'en est-t-il chez les abeilles sans dard ? Jusqu'en 1971 la question était entière, époque à laquelle nous avons entrepris les premières expériences avec les trigones africaines. Puis, nous avons élargi notre

champ de travail à une mélipone mexicaine, *Melipona beechei*. C'est le bilan de ces recherches que nous allons exposer ici.

PRINCIPES DE CES RECHERCHES

Le principe de notre expérimentation était simple : il s'agissait de modifier la quantité de nourriture déposée par les ouvrières de ces diverses abeilles pour leurs larves, et voir à l'issue de l'élevage quelles sortes d'individus allait apparaître.

Expériences avec les Trigones

Nous avons vu que chez les Trigones les cellules royales sont nettement distinctes des cellules de mâles et d'ouvrières. On sait donc, au départ, quelle est, pour le sexe femelle, la destinée des différentes larves.

Expériences de suralimentation : des larves d'âge avancé sont extraites de petites cellules (donc, larves d'ouvrières ou mâles) alors qu'elles ont terminé ou presque la ration alimentaire dont elles disposent. Elles sont suralimentées grâce à de la nourriture larvaire provenant de petites cellules juste operculées (ne contenant que des œufs ou une très jeune larve). Les larves en expérience acceptent assez facilement la suralimentation et grossissent d'une façon remarquable. Nous avons arrêté la suralimentation de ces larves lorsqu'elles eurent atteint la taille de larves de reines en fin de croissance. Mais nous nous sommes heurtés à une difficulté insoupçonnée : ces larves, gorgées de nourriture ne se sont pas métamorphosées.

Une étude ultérieure de la biologie du couvain royal de différentes trigones nous a appris que les larves de reines de ces abeilles entrent en une sorte de diapause après leur dernier repas et avant la mue nymphale. Ainsi, des prénymphes de reines, produites dans des conditions naturelles n'étaient toujours pas nymphosées après plus de 2 mois, alors que dans les mêmes conditions tout le couvain mâle ou ouvrières était éclos depuis longtemps. Cette observation contraste étrangement avec ce qui se passe chez *Apis mellifica* et même chez les mélipones, où la larve de reine a un temps de développement plus bref que celui de la larve d'ouvrière. En cela les trigones ressemblent aux bourdons.

Nous avons donc tourné la difficulté en arrêtant la suralimentation au moment où les larves dépassaient juste la taille habituelle des larves mâles ou ouvrières en fin de croissance. Dans ce cas nous avons vu se produire les nymphoses. Les résultats ont été nets. Les larves mâles ont donné des mâles géants, les larves femelles qui devaient obligatoirement donner des ouvrières, ont toutes, sans exception donné des reines. Ces reines étaient plus petites que les reines normales, néanmoins elles étaient bien constituées dans leurs caractéristiques essentielles.

Notons que nous avons obtenu ces résultats en suralimentant des larves à l'aide de nourriture provenant de petites cellules (mâles ou ouvrières) de la même espèce que les larves testées, ou bien d'espèces, et même de genre différents. La qualité spécifique de la nourriture n'intervient pas, seule la quantité semble avoir de l'importance. On a même obtenu des reines à partir de couvain d'ouvrière nourri d'un mélange miel-pollen prélevé dans les réserves du nid et non plus dans les cellules d'élevage.

Expériences de sous-alimentation : il nous a fallu ouvrir de très nombreuses ruches de trigones variées pour obtenir une très jeune larve royale dont la taille fut encore inférieure à celle d'une larve d'ouvrière en fin de croissance. Cette larve royale mise à jeun s'est métamorphosée en ouvrière.

Il est a noter que des larves d'ouvrières ou de mâles mises à jeun sont capables de se nymphoser elles aussi en donnant respectivement des ouvrières et des mâles miniaturisés.

Expériences avec les Mélipones

Le principe de nos expériences avec les mélipones était le même, à ceci près que le sexe et la caste des individus testés étaient totalement indiscernables à l'avance. Il nous a donc fallu expérimenter sur un plus grand nombre de larves et comparer les résultats obtenus avec les proportions respectives des différentes catégories d'individus venant à éclore dans les conditions naturelles au moment de nos expériences.

Expériences de sous-alimentation : nous avons pris dans différentes ruches des lots de larves n'ayant pas tout à fait fini leur ration alimentaire. Ces larves mises à jeun dans des cellules vides se sont nymphosées et ont donné soit des mâles miniatures, soit de petites ouvrières, ces dernières en proportion significativement plus grandes que dans les conditions normales. Parfois, mais exceptionnellement, on a obtenu aussi des reines miniatures. Dans le meilleur des cas toutes les larves femelles se sont nymphosées en ouvrières (100 %).

Expériences de suralimentation : ces expériences sont plus délicates à réaliser qu'avec les trigones, car les larves ayant terminé leur ration ont tendance à refuser un apport supplémentaire de nourriture. Néanmoins, on est arrivé à inverser le rapport reines/ouvrières comparé à celui des conditions naturelles. Dans le meilleur des cas on a obtenu 71,4 % de reines et 28,6 % d'ouvrières alors que la ruche d'origine fournissait à ce moment là 22,3 % de reines et 77,7 % d'ouvrières.

La suralimentation des larves a été pratiquée en injectant dans les cellules d'élevage de la nourriture prélevée au hasard dans de jeunes cellules où l'œuf n'était pas encore éclos.

Les individus obtenus lors de ces expériences avec les mélipones ont pu être classés sans ambiguïté en reines et ouvrières. Cependant, une observation attentive a permis de déceler des caractères intercastes chez un certain nombre d'entre eux. Les résultats fournis

par ces abeilles sont plus difficiles à interpréter que ceux obtenus avec les trigones. Il est vrai que l'inconnue qui pèse sur la destinée du couvain est un problème d'importance. D'autre part, on ne sait rien non plus de la composition du contenu alimentaire des cellules d'élevage avec lesquelles on expérimente. Malgré tout, l'ensemble des résultats acquis au cours de nos expériences de sous-alimentation et de suralimentation prouvent d'une façon indubitable que les facteurs alimentaires influencent le devenir des larves, tout comme chez les Trigones et chez *Apis*. Il ne semble donc pas justifié d'invoquer pour ces abeilles un déterminisme des castes par voie génétique, comme cela avait cours jusqu'ici.

Comparaison avec Apis mellifica

La nourriture larvaire des Trigones et des Mélipones est constituée de deux phases, une phase sirupeuse, à base de miel et une phase solide constituée par des grains de pollen. Lors du remplissage des cellules ces deux phases sont régurgitées en mélange homogène mais au cours de la croissance de la larve, le pollen se stratifie progressivement si bien que la larve au fur et à mesure de son évolution absorbe une pâtée de plus en plus sèche et solide. On ignore, pour l'heure, si ce processus a une signification biologique pour les larves en croissance. De toute façon, cette évolution dans le temps de la nourriture ingérée par le couvain de ces abeilles est sans commune mesure avec la complexité de l'alimentation réservée aux différentes catégories de larves d'*Apis mellifica*. Rien qu'en ce qui concerne le sexe femelle on distingue déjà plusieurs types de nourriture.

Larves d'ouvrières : elles sont nourries pendant les 3 premiers jours d'une gelée nourricière (gelée ouvrière) comprenant deux phases, une phase limpide et une phase opaque, blanche. Ces deux phases sont dans les rapports 3/1 ou 4/1. – Passés 3 jours, les larves d'ouvrières ne reçoivent pratiquement plus de la nourriture blanche mais seulement la phase limpide accompagnée d'une pâtée jaune à base de pollen. Ces deux derniers types d'aliment sont alors dans les rapports 2/3, 1/3 et constituent ce que l'on appelle la gelée ouvrière modifiée.

Larves de reines : les deux composants limpides et blancs se retrouvent tout au long du nourrissage de la larve royale dans des proportions d'environ 1/1. Toutefois, pendant les 3 premiers jours la sécrétion blanche domine puis l'inverse se produit à partir du 4ème jour où, alors, c'est le composé limpide qui est le plus abondant. On trouve seulement quelques traces de pollen dans la nourriture des larves âgées.

On estime que le composé blanc est issu des glandes mandibulaires tandis que le composé limpide est un mélange à la fois de sécrétions des glandes hypopharyngiennes et de regurgitation du miel du jabot. En somme, si on appelle gelée royale, la nourriture des larves de reines, on voit que cette dernière évolue, elle aussi, en fonction de l'âge de la larve et qu'elle est composite.

QUELQUES RÉSULTATS D'EXPÉRIENCES

De nombreuses expériences ont été tentées avec ce matériel de choix, néanmoins tout n'est pas encore dit sur le rôle joué par les divers composants alimentaires au cours de la détermination des castes d'*Apis mellifica*.

C'est Weiss qui récemment (1978) a donné les meilleures précisions quant à l'époque de fixation des castes chez les différentes catégories de larves. La larve d'ouvrière de 4 jours 1/2 peut donner une reine si on lui change sa nourriture pour de la gelée royale. (Elle s'alimente pendant 5 jours). Une larve de reine donnera une ouvrière si elle est sous alimentée et ce, pratiquement jusqu'à la fin de sa période de consommation de nourriture qui, pour elle, dure un peu plus de 5 jours.

Chez *Apis*, ces expériences de modification de nourriture larvaire entraînent parfois l'apparition d'intercastes. C'est l'ovaire qui est le premier à réagir à un supplément de nourriture royale en accroissant le nombre des ovarioles. En revanche, les caractères morphologiques externes (pattes, mandibules etc.) sont affectés plus tardivement.

CONCLUSION

Il ressort de ces travaux et des nôtres, qu'*Apis*, Trigones et Mélipones sont susceptibles de réagir à des changements alimentaires, presque jusqu'à la fin de leur période d'alimentation en modifiant plus ou moins, mais souvent d'une manière totale leur devenir initial. La caste ne se fixe donc qu'au cours du stade V, le dernier, et même, parfois en fin de celui-ci. La plasticité de ces larves est donc appréciable. Quels sont les facteurs alimentaires qui infléchissent le devenir des larves ?

Aussi surprenant que cela puisse paraître, malgré toutes les analyses qui ont pu être faites des différentes nourritures larvaires d'*Apis*, on ne connait pas à l'heure actuelle le rôle précis des divers constituants dans la détermination des castes. L'acide pantothénique, la bioptérine, qui sont des composants très caractéristiques de la gelée royale et à des taux remarquables, ne se sont pas révélés à l'analyse comme les agents déterminants de l'apparition des reines.

Au cours de diverses publications Dietz et coll. ont indiqué que la variation du taux d'humidité de la nourriture larvaire jouerait un rôle dans l'obtention des reines, toutefois ces résultats sont contestés par Weaver (1974) qui a observé que les larves élevées avec de la gelée royale pouvaient supporter sans dommages apparents diverses modifications de composition de leur

gelée nourricière. Cet auteur souligne entre autres l'intérêt d'un apport de sucres pour améliorer les rendements de l'élevage. Par ailleurs, des recherches concomittantes et indépendantes de Weiss (1975) et de Asencot & Lensky (1976) viennent de montrer qu'une adjonction de sucres à de la simple gelée d'ouvrière suffit à produire à partir de larves d'ouvrières des intercastes et même des reines. D'après les derniers auteurs, le sucre interviendrait, peut-être, comme phagostimulant.

Enfin, il semble bien démontré que la gelée d'ouvrière (celle qui est donnée à la toute jeune larve) est incapable d'assurer seule un développement complet de quelque caste que ce soit ; les larves nourries uniquement avec elle meurent toutes avant la nymphose.

Tout ceci ne représente qu'un petit aperçu de la somme des données que l'on possède à l'heure actuelle sur ce sujet chez *Apis mellifica*. Toutefois, ces masses d'informations sont relativement disparates et encore difficiles à coordonner. Bien qu'on reconnaisse à la nourriture un rôle initiateur essentiel dans la détermination des castes jusqu'ici, on attend encore le fin mot de l'explication.

Rien d'étonnant par conséquent que les recherches encore fort peu nombreuses chez les abeilles sans dard n'aient pas livré tous leurs secrets. D'ailleurs, il n'est pas exclu de penser que des études comparées entre ces diverses abeilles permettraient peut-être d'accéder plus rapidement à la connaissance que nous cherchons. Les études actuelles d'endocrinologie chez diverses abeilles sociales permettent de se faire une idée des schémas physiologiques sur lesquels est basé le déterminisme des castes. Reste à définir encore la nature véritable des mécanismes trophiques qui président à leur mise en place.

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ENDOCRINE REGULATION OF CASTE DETERMINATION IN ANTS

L. PASSERA

Laboratoire Associé au C.N.R.S. n° 333
Recherche Coopérative sur Programme du C.N.R.S. n° 645
Laboratoire de Biologie des Insectes, Université Paul-Sabatier
118, route de Narbonne, 31062 Toulouse Cedex France

SUMMARY

Research work carried out on *Solenopsis invicta, Myrmica rubra, Pheidole pallidula, Plagiolepis pygmaea* and *Aphaenogaster senilis* has pinpointed the role played by hormones at the moment of caste determination in ants.
Role of the JHA's : in strong concentrations they delay metamorphosis and cause morphogenetic problems which can eliminate the brood. At lower levels they play a role in sexualization of the larvae. The JHA's administered either by mixing with the food, or given as a topical application, or by means of injections bring about the production of sexual larvae, mostly females, in the colony. The stages which are sensitive to JH vary according to the species. *Pheidole pallidula* is sensitive the earliest, determination occuring during ovogenesis ; in *Solenopsis invicta* larvae in the first stage react to the introduction of JH, whereas in *Myrmica rubra* this occurs in the last larval stage. Ligature and removal of the *corpus allata* (CA) (*Myrmica*), use of Precocen (*Pheidole*) eliminate the CA's or prevent their action thereby favouring the appearance of workers.
Role of ecdysteroids : the use of ecdysone (*Myrmica*) or of ecdysterone (*Pheidole*) dramatically lowers the percentage of sexual larvae. It can also be observed that in *Pheidole* the level of ecdysteroids is higher in the queens laying eggs with worker orientation than in those laying eggs with sexual orientation. The same is true of the eggs themselves.

The juvenile hormones and the ecdysteroids thus have antagonistic roles. Their relative variations which are controlled by external factors, such as the composition of the colony or climatic conditions determine the orientation of the brood.

RÉSUMÉ

Régulation endocrine de la détermination des castes chez les fourmis

Les travaux effectués chez *Solenopsis invicta, Myrmica rubra, Pheidole pallidula, Plagiolepis pygmaea* et *Aphaenogaster senilis* conduisent à préciser le rôle joué par les hormones lors de la détermination des castes chez les fourmis.
Rôle des JH : à forte concentration, elles retardent la métamorphose et déterminent des troubles morphogénétiques pouvant faire disparaître le couvain. A doses plus faibles elles ont un rôle dans la sexualisation des larves. Les JHA distribués soit mélangés à la nourriture, soit par applications locales ou encore par injections entraînent la formation de larves sexuées, surtout femelles, dans la société. Les stades sensibles à la JH sont variables selon les espèces. *Pheidole pallidula* est la plus précoce, la détermination se produisant pendant l'ovogenèse ; chez *Solenopsis invicta* c'est la larve du premier stade qui réagit à l'apport de JH, alors que chez *Myrmica rubra* c'est celle du dernier stade. Les ligatures et allatectomies (*Myrmica*), l'utilisation du Précocène (*Pheidole*) en éliminant les CA ou en bloquant leur fonctionnement favorisent au contraire l'apparition des ouvrières.
Rôle des ecdystéroïdes : un apport d'ecdysone (*Myrmica*) ou d'ecdystérone (*Pheidole*) diminue fortement le pourcentage des larves sexuées. Chez *Pheidole* on note d'ailleurs que le taux des ecdystéroïdes est plus élevé chez les reines pondeuses d'œufs à orientation ouvrière que chez celles pondeuses d'œufs à orientation sexuée. Il en est de même pour les œufs eux-mêmes.

Les hormones juvéniles et les ecdystéroïdes ont ainsi un rôle antagoniste. Leurs variations relatives réglées par les facteurs externes comme la composition des sociétés ou les conditions climatiques déterminent l'orientation du couvain.

INTRODUCTION

The study of caste determination in ants has been mainly centred, over the last few years, around the importance of social factors (composition of societies) and environmental restrictions (climatic factors). The best known species in this respect are the *Formica* of the group *rufa* (Gösswald et Bier, 1953, 1954a, 1954b ; Bier, 1954, 1958 ; Schmidt, 1974), *Myrmica rubra* (Brian, 1974a, 1979), *Leptothorax nylanderi* (Plateaux, 1971) et *Plagiolepis pygmaea* (Passera, 1969, 1974). From these investigations and those concerning 20 or so other species, the following general rules can be drawn :

– Orientation usually occurs at the last instar suggesting trophogenic determinism (with one exception) ;

– The queen or queens have an inhititing action, of varying degree, on the development of potential queen larvae.

– The winter or seasonal dormancy period of the nursing workers and of the larvae (societies with a dorman brood) is indispensible for the appearance of sexual brood.

– The larvae are orientated by the workers wich give a diet adapted to the chosen caste.

These investigations tell us WHEN and HOW a larva becomes orientated towards one caste or another but studies giving an indication of WHY are much more rare. Attention is required not in the direction of the whole colony but rather towards the individual and in particular its physiology.

CYTO-ANATOMICAL DATA

In adults

In various species the size of *corpora allata* was studied and authors found that the volume of the glands was proportional to the size of the ants : they are larger in queens that in worker (Hultin, 1947 ; Gawande, 1968 ; Bressac and Bitsch, 1969).

In larvae

In *Myrmica rubra*, Brian (1959) noted that the CA of the queen larvae – although larger than those of the workers in absolute terms – are no longer so when considered in relative terms. A similar modifications was noted by Lappano (1958) in the larvae *Eciton burchelli* a species with widespread polymorphism among the workers : the size of the CA is directly proportional to that of workers themselves.

In *Plagiolepis pygmaea* (Suzzoni and Grimal, 1981), the results are as follows :

Worker biased larvae : the absolute volume remains almost stable (about 4 000 μm^3) throughout the determination phase (fig. 1). The weight increase of the larvae during this period being moderate, the weighted volume of the CA decreases fairly slowly (fig. 1). The number of cells seems to be constant varying between 7 and 8. The cell volume (fig. 2) is fixed between the end of hibernation and the pharate pupal stage at 500 μm^3.

Queen biased larvae : the absolute volume (fig. 3) increases three fold going from 3 000 μm^3, when activity starts again, to 9 500 μm^3, at the pharate pupal stage. The ratio is therefore 1.7 in favour of queen larvae. The growth of the sexed larvae being particularly rapid, the weighted volume (fig. 3) decreases faster than in worker larvae. The number of cells increases slightly

from 7 or 8 to 9 or 10 but the most remarkable fact is that the cell volume passes from 500 to 1 240 μm^3 (fig. 2). Overall, it can be noted that the characteristics of the CA in both series show differences which could be explained by differing physiological activities.

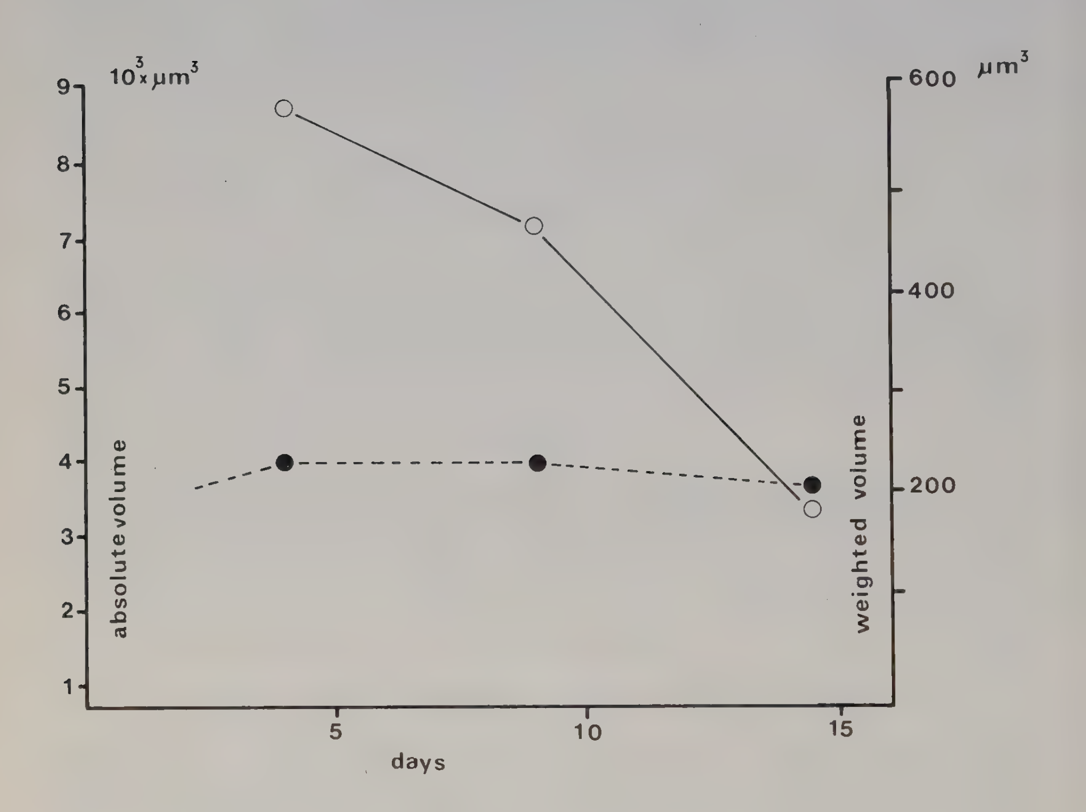


Fig. 1 — Corpora allata volume of the worker-biased larvae according to the age from the end of the hibernation to the naked prenymph stage (*Plagiolepis pygmaea*). Broken line : absolute volume in 10^3 μm^3. Solide line : weighted volume in μm^3. From Suzzoni and Grimal (1981).

Fig. 1 — Volume des corps allates des larves-ouvrières en fonction de l'âge depuis la sortie d'hibernation jusqu'au stade prénymphe chez *Plagiolepis pygmaea*. Trait pointillé : volume absolu en 10^3 μm^3 ; trait plein : volume pondéré en μm^3. D'après Suzzoni et Grimal (1981).

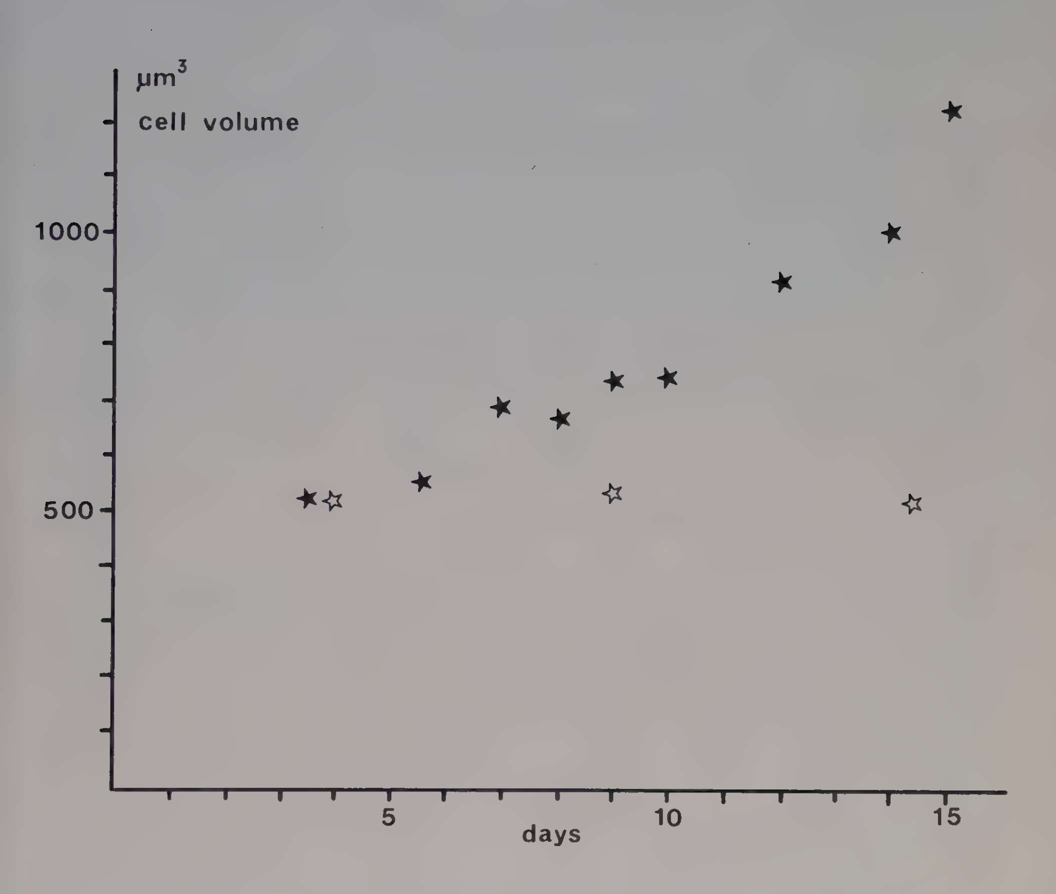


Fig. 2 – Evolution of the mean cellular volume (absolute volume /cell number per corpus allatum) in μm^3 during the development between the end of hibernation and the naked prenymph stage (*Plagiolepis pygmaea*). Black stars : queen-biased larvae ; white stars : worker-biased larvae. From Suzzoni and Grimal (1981).

Fig. 2 – Evolution du volume cellulaire moyen (volume absolu/nombre de cellules par corps allate) en μm^3 au cours du développement depuis la sortie de l'hibernation jusqu'au stade prénymphe chez *Plagiolepis pygmaea*. Etoiles noires : larves à orientation reine ; étoiles blanches : larves à orientation ouvrière. D'après Suzzoni et Grimal (1981).

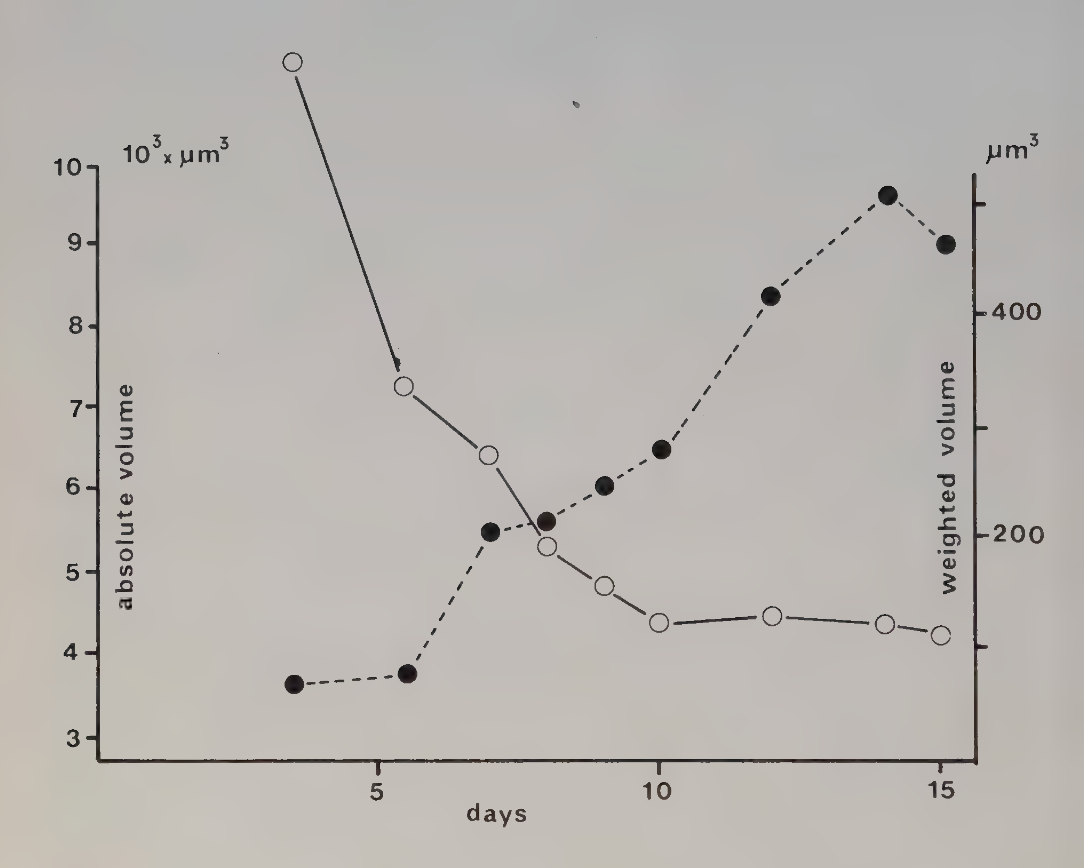


Fig. 3 – Corpora allata volume of the queen-biased larvae according to the age from the end of the hibernation to the naked prenymph stage (*Plagiolepis pygmaea*). Broken line : absolute volume in 10^3 μm^3 ; solid line : weighted volume in μm^3. From Suzzoni and Grimal (1981).

Fig. 3 – Volume des corps allates des larves-reines en fonction de l'âge depuis la sortie d'hibernation jusqu'au stade prénymphe chez *Plagiolepis pygmaea*. Trait pointillé : volume absolu en 10^3 μm^3 ; trait plein : volume pondéré en μm^3. D'après Suzzoni et Grimal (1981).

THE ACTIVITY OF THE JUVENILE HORMONES

The case of *Myrmica rubra*

Topical applications and injections

Brian (1974b, 1976) used post-wintering larvae wich are queen-potential. They received JHA's as topical applications or as injections. Metamorphosis was clearly retarded in all treated larvae. All the nymphs obtained from both treated and control larvae were queens but the former weighed more than the latter. In another series of experiments the author choose average-sizes post-wintering larvae known to have less chance of developping into queens than their larger counterparts. Here, he obtained 84 % queen nymphs in the treated group and only 60 % in the controls. So JH analogues retard metamorphosis, prolong the growth period – and thus increase the size of the queens – and increase the percentage of larvae which become transformed into queens.

Ligature and corpus allatum *extraction*

Comparison of the imaginal discs of legs and wings : the large post-wintering larvae used in these tests are queen-potential and so possess imaginal wing discs. The degree of sexualization of the larvae can be judged by measuring the surface areas of the wing buds and comparing them with those of the leg buds 6 days after treatment : as sexualization increases the rate of growth of the imaginal wing discs increases whereas that of the legs is slowed down.

The treated larvae either undergo cephalic ligature short-circuiting the CA or removal of the CA. Under these conditions, the surface area of wing buds in the control animals was either equal to that of the leg buds (60 % of the cases), or bigger (in 40 % of cases), and was never smaller ; the wings develop therefore more quickly than the legs. On the other hand in the group of treated animals the surface area of the wing buds was either equal to that of the leg buds (in 33 % of cases) or smaller (in 67 % of cases) and was never larger ; therefore the absence of the CA or their short-circuiting causes an stoppage in the inhibiting action controlling growth and differentiation of the legs.

Leg segmentation : in this experiment the development of the imaginal leg discs was estimated by counting the number of segments ; rapid segmentation taking place at the expense of imaginal wing disc growth indicating a difficult or at least retarded sexualization. The results show that for cephalic ligature isolating the CA, a much higher degree of segmentation is noticeable

than in the control group. Furthermore it is possible to retard the differentiation of the legs by immersing the ligatured animals in solution of JH analogues. These experiments confirm the previous ones as to the role of JH ; it retards growth of the leg buds in favour of growth of the wing buds. JH has therefore a positive action on sexualization.

The case of *Aphaenogaster senilis*

Topical applications of a JHA are performed on larvae of varying ages in the presence of their queen (Ledoux, 1976). In the control group the queen caused total inhibition, only workers resulted. In the treated group the appearance of gynaecoid workers and even a few nymphs was observed.

The case of *Solenopsis invicta*

Action on mortality and morphogenesis

Cupp and O'Neal (1973), Vinson et al. (1974), Troisi and Riddiford (1974), Vinson and Robeau (1974) treated a brood of *Solenopsis* with two JHA's, ZR 512 and ZR 515 (methoprene). The results concerne the action on larval mortality and disturbances noticed during metamorphosis. Larvae develop into nymphs without legs or antennae, sometimes having large mandibles without teeth. Some of these nymphs develop into imagos which are carriers of abnormalities, in particular with relation to the legs.

Action on caste

By submitting the colony to the action of JHA, Troisi and Riddiford (1974) obtained noteworthy results concerning the equilibrium of the societies. ZR 512 injected at the rate of 100 μg/cockroach fed per week results in fewer larvae but, more important, it was noticed that 10 days after the beginning of this treatment 75 % of the larvae were of the sexual type, most of them developing into males ; the workers only forming 25 % of the total. With an even lower dose (10 μg/cockroach per week) the number of larvae produced becomes normal again and the brood is composed of 25 % males against 75 % workers. In all these cases the colonies both before the beginning and after the end of treatment only produced workers. As to ZR 515, it appears that although it too lowers the larval population it seems less effective in producing winged animals. If the drop in larval production can be explained by the action of JHA on the larvae, the appearence of numerous males at the

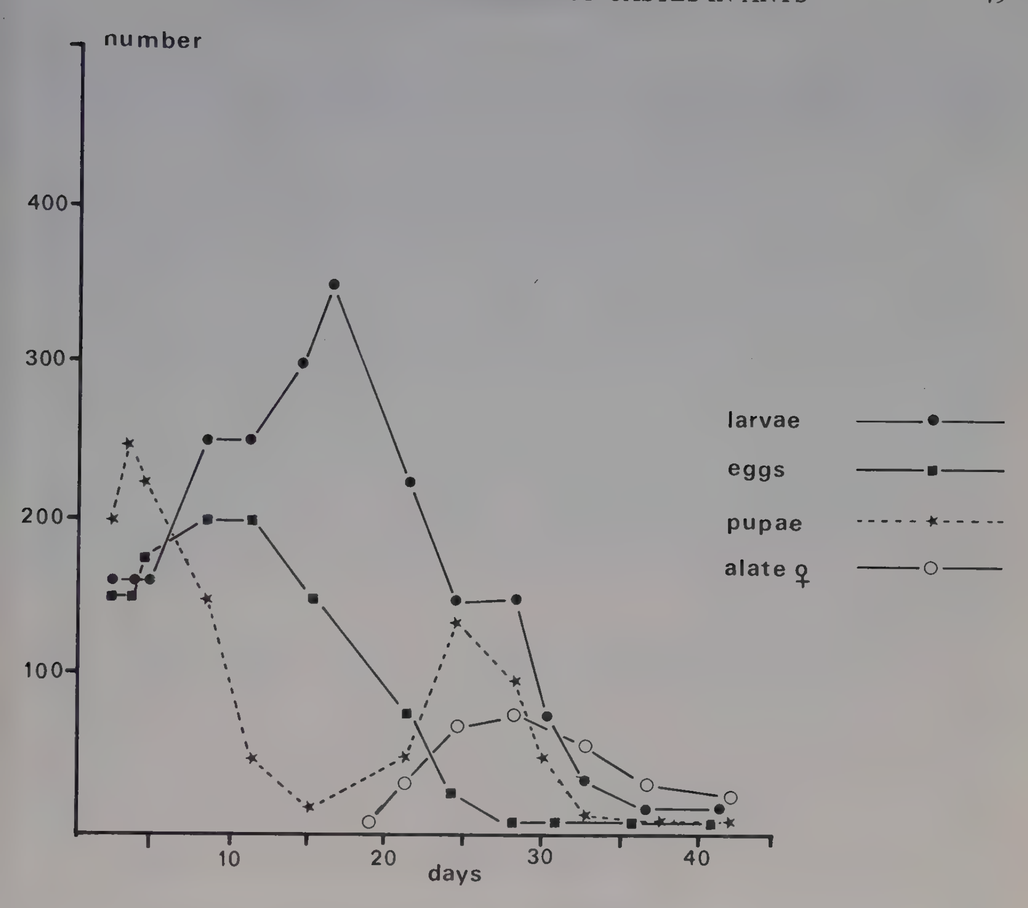


Fig. 4 – Number of imported fire ants in each stage after feeding the colony doses of JHA in soybean oil (50 mg/colony). From Vinson and Robeau (1974).

Fig. 4 – Evolution numérique du couvain de *Solenopsis invicta* dans une société nourrie avec de l'huile de soja contenant des analogues de la JH (50 mg/colonie). D'après Vinson et Robeau (1974).

expense of workers tends to indicate an action on the queen which would then lay unfertilized male eggs.

The use by Vinson and Robeau (1974) of 6 JHA's mixed with food in doses varying from 0.05 to 50 mg/ml provides interesting results. Whatever JHA used, at whatever dose there is always production of sexual larvae 20-30 days after the beginning of the treatment (fig. 4). In the controls sexual larvae were never produced, these colonies always being quite young. Like the rest of the brood large numbers of these larvae died before the nymph

stage ; those that survived and reached the nymph stage were all queens and nymphosed into winged queens. This result is obviously different to that of Troisi and Riddiford who obtained males. Thus incorporation of JHA into the food has the effect of sexualizing a part of the brood of *Solenopsis*.

In a subsequent phase the same authors (1976) attempted to determine whether the sexualization of the brood is due to an effect of the JH on the queen and the nature of the eggs laid or if the effect takes place later, during the larval stages. To this end they treated the queen of a colony by topical application. After a 2 days pause in laying, the eggs produced developed normally and the larvae all become workers. In another series of tests, the colonies possessing a brood in all stages but lacking their queen were treated by JHA. In the days that followed a drop in the number of larvae and nymphs of «minor» workers was noticed, followed by their disappearance ; during this time however larvae and nymphs of major workers and queens were produced. In the control colonies there was never production of either «major» workers or queens. The absence of sexualization when only the queen was treated lead one to think that the JH does not act during ovogenesis, but later during larval development.

Banks et al. (1978) looked for the stage which is sensitive to the action of JH. The eggs laid in a colony fed with JH oil solution were separated into 2 groups ; the first was reared by workers which were fed normally ; they all gave rise to worker nymphs ; the second group was reared by workers which were fed JH and it resulted in sexual larvae. Therefore JH has no action at all on queens or on eggs. Furthermore larvae in the third or fourth stages present in the nest at the time of treatment developed into worker larvae. It appears therefore that the first larval stage and perhaps the second are sensitive to action by JHAs.

Distribution and circulation of JH

The distribution and circulation of the JHA's in the colonies was followed using radioactive analogues (Wendel and Vinson, 1978 ; Bigley and Vinson, 1979). In the case of topical applications the rates of absorption, then of degradation and lastly of excretion are found in the following decreasing order : workers, larvae, nymphs and prenymphs, each category having a means of degradation of its own. When the JHA is mixed with the food the workers are immediately contaminated and then lose the compound at a steady rate of which only the metabolites are found 34 days later (fig. 5). The larvae presented maximum contamination 1.5 days after the introduction of the radioactive JHA ; they had at that point 7 % of the total radioactivity which they then lost progressively. Althought it appears normal that the nymphs

which are not fed are pratically free from contamination, it is more suprising in the case of the queens. In any case it confirms that JH acts on the larvae and not on the queen since she is not involved in the circulation of the labelled product.

Briefly, JHA's introduced into a colony have a double action in *Solenopsis invicta* :

– Actions on metamorphosis : they bring about the disappearance of developing «minor» worker larvae and nymphs and determine morphogenetic abnormalities of rescued nymphs ; in addition at high doses they can slow down or stop the queen laying ;

– Action on the determination of castes : if the dose administered is moderate enough to allow the queen to lay, the larvae which develop will give rise to «major» workers but above all sexual males and/or females.

The appearance of winged males implies an action on the queen which then lays unfertilized eggs ; the appearance of winged females results from action by the JHAs on the young brood in the first or second stages, the queen no longer being concerned.

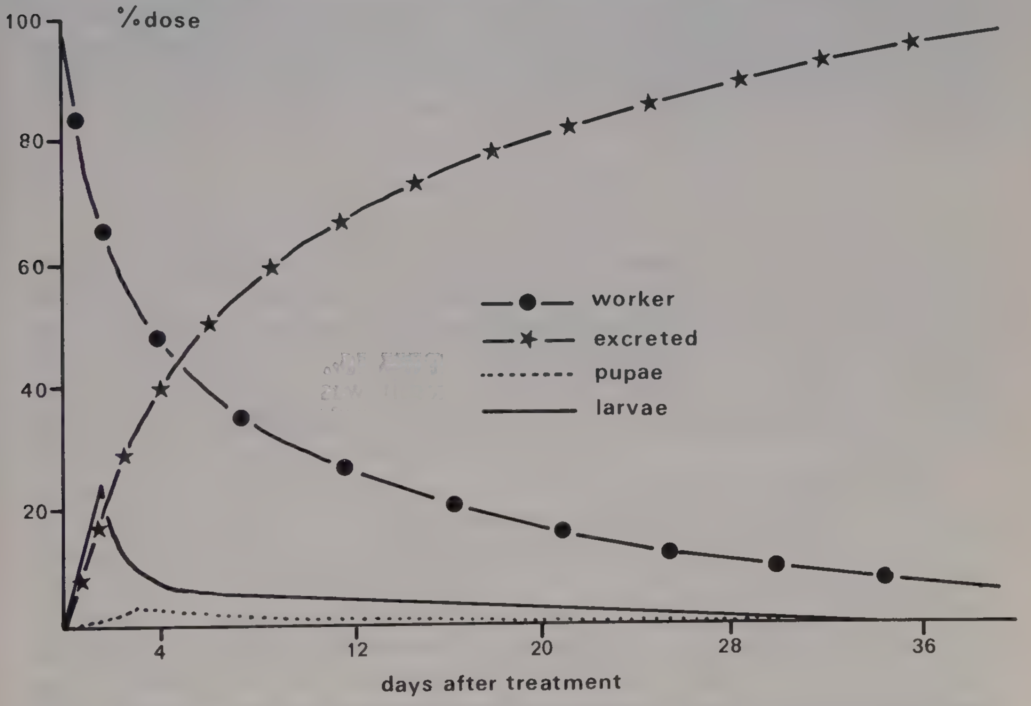


Fig. 5 – Distribution of radioactivity after feeding of the juvenile hormone analogue R-20458 formulated in soybean oil to adults within colonies of the imported fire ant. From Wendel and Vinson (1978).

Fig. 5 – Evolution de la radioactivité dans des colonies de *Solenopsis invicta* nourries avec de l'huile de soja contenant un analogue de la JH (R-20458). D'après Wendel et Vinson (1978).

The case of *Pheidole pallidula*

Sexual individuals result here from the first brood of spring : at the end of hibernation most of the queens lay biased eggs which all develop into sexed larvae, even in bad breeding conditions. Later the eggs are all worker biased (Passera, 1980). This characteristic makes it possible to use eggs with a known future : sexual or workers.

Treatment of whole societies

Whole societies were experimented on more than one month after the end of hibernation, that is to say when they were only producing worker or soldier broods. They were fed with *Tenebrio* larvae which had received an injection of 10 μg of a JHA (Ayerst's AY 22, 342, a mixture with 8 isomers of JHI). The eight societies treated produced a sexed brood between the second and sixth week following the beginning of the treatment whereas the controls only produced worker and soldier broods (Passera et Suzzoni, 1978a).

Treatment of queens

JHA dissolved in acetone or olive oil was used in topical applications at weekly doses of 1 μg, 0.1 μg or 0.01 μg (Passera and Suzzoni, 1978b, 1979a). The treatments were carried out one month after the end of hibernation, after the period during which the sexual brood appeared. 28 colonies out of 29 once more gave rise to sexual larvae. The result was especially remarkable for the 11 colonies which had not given rise to sexual larvae at the end of hibernation.

The controls however continued to produce workers. Sexualization appears not to depend on the nature of the solvent but rather on the dose of JHA (fig. 6), 0.01 μg is close to the effect threshold. More often than not sexed larvae appeared during the third week following treatment ; this rather long interval shows that JHA acts on queens during ovogenesis ; indeed if it were a case of action on the larvae the effect would be immediate ; there being brood at all stages when the first application was given. Besides, eggs collected during the few hours quarantine undergone by the queens at the time of each treatment, develop in part into sexual larvae when they are placed in untreated queenless colonies. Therefore the ovary in the queens appears to be sensitive to the hormone environment.

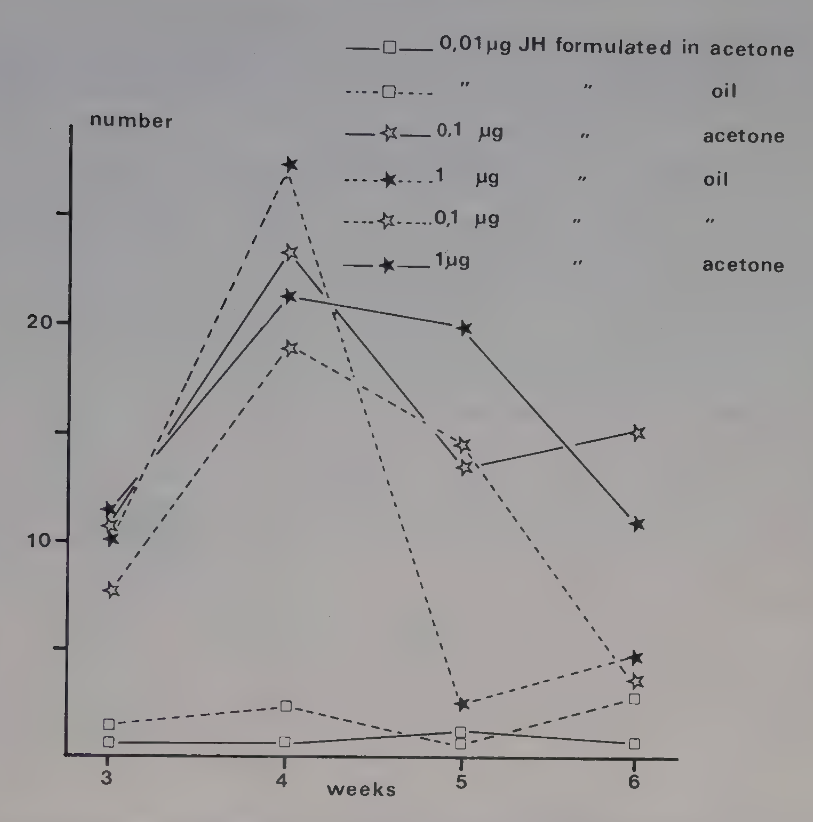


Fig. 6 —Effets of topical applications on queens (*Pheidole pallidula*) according to mode of JH administration. Along the abscissae : number of weeks after the beginning of the treatment. Along the ordinates : average number of sexual larvae produced in each treatment.

Fig. 6 — Effets des applications topiques des reines de *Pheidole pallidula* en fonction des modes d'administration de la JH. En abscisses : nombre de semaines après le début du traitement ; en ordonnées : nombre moyen de larves sexuées produites pour chaque traitement.

Treatment of the brood

Brood taken from colonies producing workers and soldiers is distribued to colonies of queenless workers. The eggs and the larvae of the three stages were immersed in a 0.5 % solution of JHA (Passera and Suzzoni, 1979a) for a few seconds. When eggs were the subject of the treatment, sexual larvae resulted six times out of seven. On the other hand treated larvae of the first, second and third stages only gave rise to workers. It appears then that JH acts only on eggs, either during ovogenesis, before laying, or during embryogenesis.

However the larvae of the three stages, whether they were treated directly of fed by treated workers showed no tendency to sexualization. The caste is therefore finally fixed in the egg in *Pheidole pallidula.*

A comparison of the activity of the 3 JHs and the anti-JHs

Weekly applications of 0.1 μg of JHI, JHII and JHIII were carried out on queens which belonged to societies producing worker biased larvae. Over a period of 5 weeks larvae were collected as soon as they became identifiable. As before, sexualization of the brood was obtained (Passera and Suzzoni, 1979b). It can clearly be seen (fig. 7) that when the average number of sexual larvae collected every week in the different colonies is

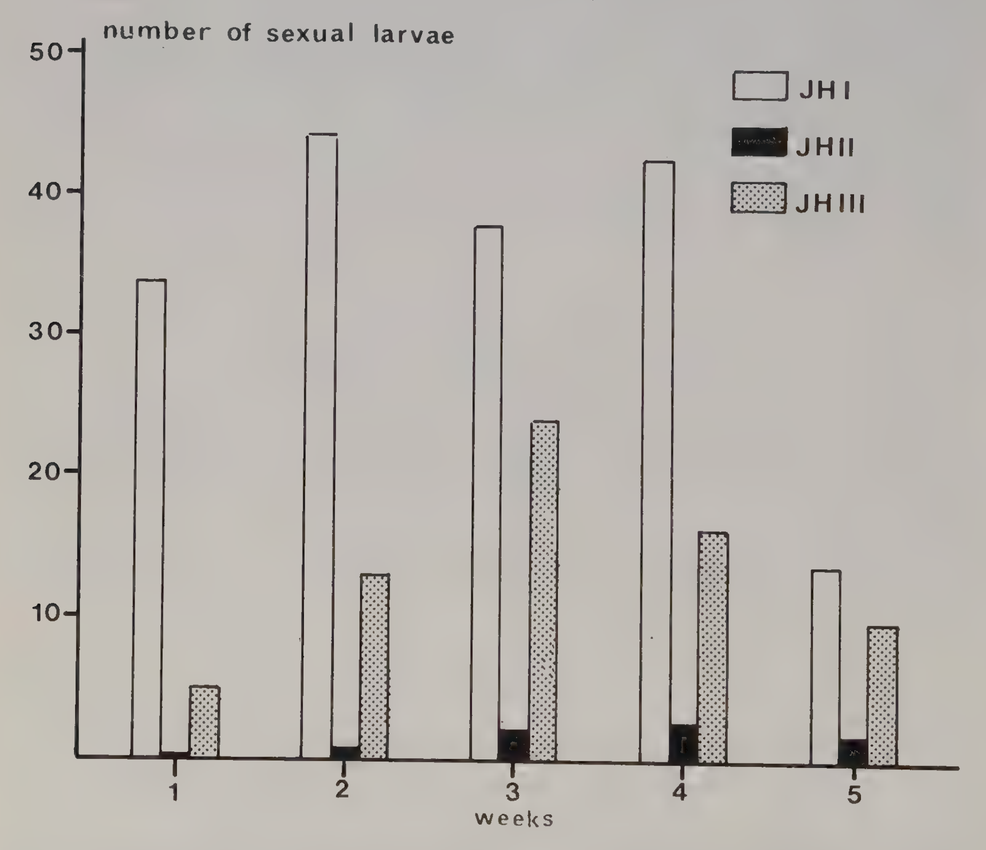


Fig. 7 – Compared effects of JHI, JHII and JHIII on appearance of sexual larvae after topical treatments on the queens (*Pheidole pallidula*). Along the abscissae, the weekly date. Along the ordinates, the number of sexual larvae produced (average by colony).

Fig. 7 – Action comparée des JHI, JHII et JHIII sur l'obtention de larves sexuées après applications topiques des reines de *Pheidole pallidula.* En abscisses, les relevés hebdomadaires ; en ordonnées, le nombre de larves sexuées obtenues (moyenne par élevage).

compared, JHI is the most effective. Each culture treated with JHI produced on average 172 sexual larvae whereas, under the same conditions, only 68 were obtained with JHII. If the results are expressed as percentages of sexual larvae with respect to the whole brood 53 % of the brood were sexual with JHI, 1,6 % with JHII and 24.7 % with JHIII.

The role of the *corpora allata* appears to be fundamental in the formation of castes in *Pheidole pallidula.* The very small size of the queens made excision of the CA impracticable and this difficulty was overcome by the use of topical applications of Precocene II, a substance which brings about degeneration or atrophy of the CA. The queens were treated twice during hibernation, once at the time of the break in hibernation and once two days later (1.5 μg Precocene : 1 μl Acetone). After 3 days of laying the queen was eliminated and the composition of the brood noted. Whereas 79 % of the untreated nests yield sexual larvae after hibernation this percentage fell to 33 % in the case of cultures treated with Precocene. If one considers the number of sexual larvae collected with respect to the total brood produced, 54 % sexual larvae were present in the untreated cultures as against 7 % in treated cultures. These figures suggest an inhibitory action by Precocene but they must be interpreted with caution because acetone which was used as the vehicle also lowers the sexualization of the brood. *Pheidole pallidula* was shown to be fairly different to *Myrmica* or to *Solenopsis.*

– at the doses used no action, either on metamorphosis or on morphogenesis, was noticed : in particular intercastes never appeared ;

– the sensitive stage is very early because sexualization results from an intervention during ovogenesis. The larval stages are not involved, as opposed to observations made on *Myrmica* or *Solenopsis.*

ACTIVITY OF ECDYSTEROIDS

The case of *Myrmica rubra*

Ecdysone in solution

Large post wintering larvae with queen potential were injected with a solution of ecdysone in a water-ethanol mixture. In 9 groups out of 14 metamorphosis occurs earlier and in 3 groups Brian (1974b) obtained a higher percentage of workers (44 %) than in the control groups (9 %).

Crystallized ecdysone

In this experiment 1 to 2 μg of ecydsone in its crystalline form was implanted per post-wintering larva. The early treatment of larvae during the pre-segmentation period appears to be ineffective. On the other hand a later

implantation during the segmentation period gave a double result : metamorphosis is accelerated and a higher proportion of workers and a lower number of queens was obtained. Therefore in the treated groups 29 % worker nymphs, 47 % intercaste nymphs and 24 % queen nymphs were obtained as opposed to 11 %, 33 % and 56 % respectively, in the control groups. Furthermore queens obtained after treatment were very small and can be considered as microgynes. The sum up, ecdysone treatment leads to early metamorphosis and favours the appearance of workers whereas the few queens produced were very small.

The case of *Pheidole pallidula*

Treatment of queens by topical application at the end of hibernation, when they are potential layers of sexual eggs, was carried out using ecdysterone dissolved in a mixture of acetone and ethanol. The fertitily of the queens does not appear altered because their average production during the first 5 days following hibernation was the same in the treated cultures and in the control cultures. On the other hand the differences concerning the construction of the castes are significant because an important drop was noticed in the number of cultures with sexed progeny : 69 % for untreated cultures as against 31 % for cultures treated with ecdysterone. The average number of sexed larvae per culture fell from 37 in the controls to 11 in the treated groups. Ecdysteroids appear to slow down the sexualization of the brood thus opposing the action observed with JH.

This hypothesis received some support from a study aimed at assaying ecdysteroids using radio-immuoassay techniques with microdialysis (Suzzoni, Passera, Strambi, 1980). The queens which laid worker biased eggs showed higher levels of ecdysteroids and other substances co-migrating with ecdysone and ecdysterone than the queens which laid queen biased eggs (fig. 8). The same assays carried out on eggs with different potentials and laid at different points in the cycle also support this hypothesis (fig. 9).

– like the queens, it was the worker biased eggs that were richest in ecdysteroids ;

– the comparison of worker biased eggs laid at the beginning of the season, with other laid in the middle of the season show that the latter possess more ecdysteroids than the former. Furthermore it is in the middle of the activity period that the ant nest produces most workers.

Therefore in *Pheidole pallidula* the appearance of sexual larvae seems to be assisted by a high level of JH whereas the appearance of workers coincides with a high level of ecdysteroids.

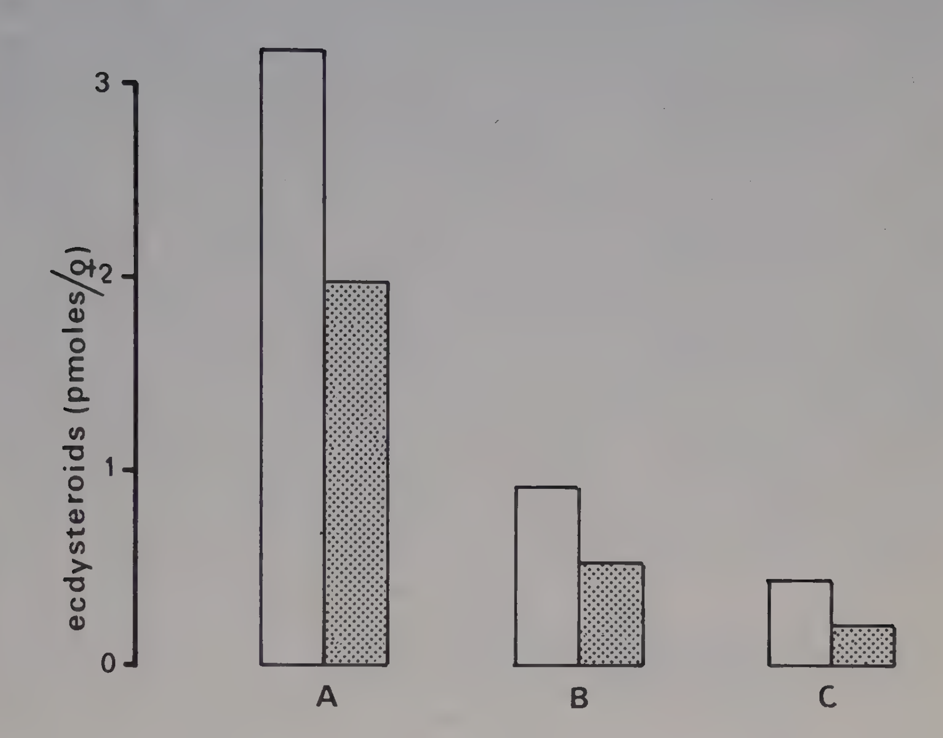


Fig. 8 — Ecdysteroid titred in queens (*Pheidole pallidula*) expressed as pmoles of ecdysterone equivalent per 1 queen. A : total ecdysteroids — B : ecdysone — C : ecdysterone. Open bars : queens laying worker-biased eggs. Spotted bars : queens laying queen-biased eggs.

Fig. 8 — Dosages des ecdystéroïdes chez les reines de *Pheidole pallidula* exprimés en pmoles d'équivalent ecdystérone pour une reine. A : ecdystéroïdes totaux — B : ecdysone — C : ecdystérone. Colonnes blanches : reines pondeuses d'œufs à orientation ouvrière. Colonnes pointillées : reines pondeuses d'œufs à orientation sexuée.

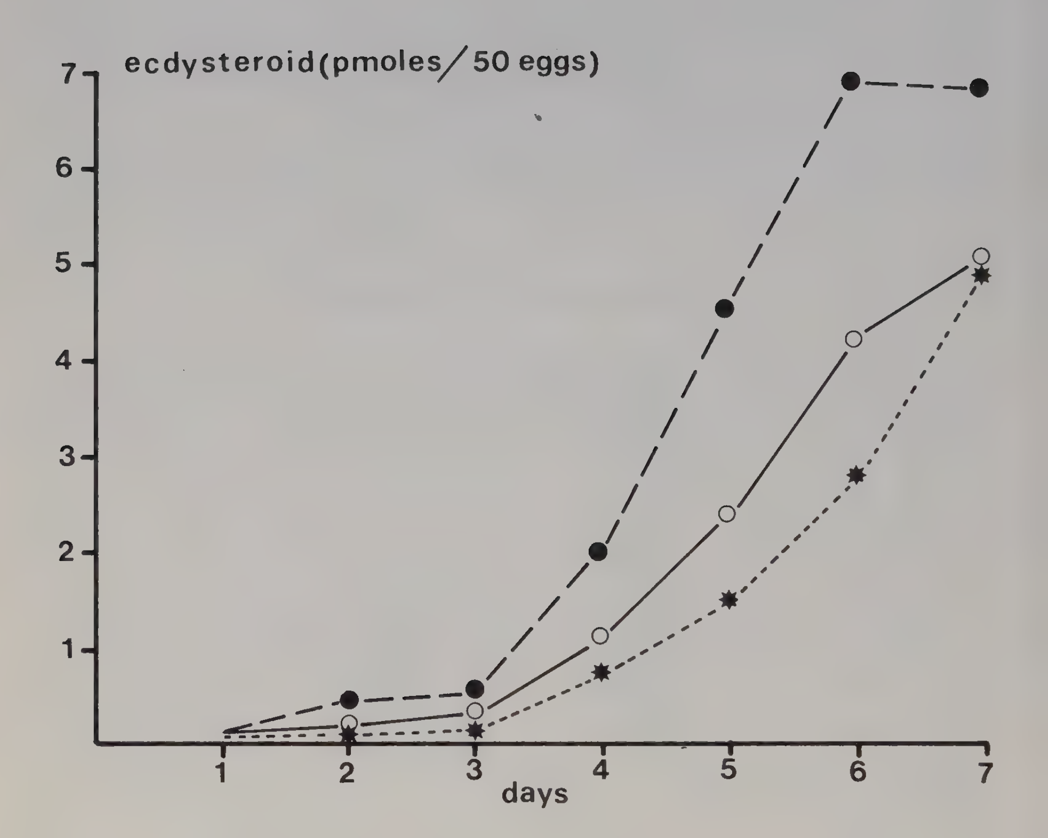


Fig. 9 – Evolution of the ecdysteroid rates during the embryonic development (*Pheidole pallidula*). Ordinate : ecdysteroids in pmoles equivalent-ecdysterone per 50 eggs. Abscissa : age in days. Spotted line : queen-biased eggs laid at the end of hibernation ; solid line : worker-biased eggs laid at the end of hibernation ; broken line : worker-biased eggs laid 1 month later.

Fig 9 – Evolution du taux des ecdystéroïdes pendant le développement embryonnaire (*Pheidole pallidula*). Ordonnées : ecdystéroïdes en pmoles d'équivalent ecdystérone pour 50 œufs ; Abscisses : l'âge des œufs en jours. Traits pointillés : œufs à orientation sexuée pondus à la fin de l'hibernation ; traits continus : œufs à orientation ouvrière pondus à la fin de l'hibernation ; traits interrompus : œufs à orientation ouvrière pondus 1 mois plus tard.

DISCUSSION

The sex determination role played by JH's appears well-established in experimental conditions in several ants. It is generally consistant with that found in other social Hymenoptera : *Apis* (Wirtz and Beetsma, 1972 ; de Wilde, 1976 ; Goewie, 1978 ; Beetsma, 1979), *Bumblebees* (Röseler, 1977), *Melipons* (Velthuis and Velthuis-Kluppel, 1975 ; Campos, 1978), *Trigons* (Campos, 1979). The phenotypic expression of caste could result from the activation of «queen» genes by juvenile hormone.

The point in the cycle where the biological material becomes sensitive to the JH is variable according to the species. In *Pheidole pallidula* it is the earliest because the JH must be supplied during ovogenesis, therefore via the material organism. In *Solenopsis invicta* only larvae in the first stage and perhaps in the second are affected. The same is found in *Aphaenogaster senilis*, the earlier stages being more readily affected by JH than the later stages. Lastly, in *Myrmica rubra* however, it is the third and fourth stages which can be affected. The sensitive period must, furthermore, be very short and difficult to determine. Without doubt this is what explains the failures experienced using certain species whose brood orientation it has so far been impossible to modify inspite of massive doses of JHA : e.g. *Plagiolepis pygmaea, Temnothorax recedens, Solenopsis fugax, Iridomyrmex humilis* (Passera and Suzzoni, unpublished).

Until now it has only been possible to study the action of exogenous juvenile hormone in ants. A supplementary proof could be provided by assaying the endogenous JH's circulating at different moments of the cycle as has been done in *Apis* (Lensky et al., 1978) but the difficulty of obtaining a large enough volume of material in *Pheidole* is a serious obstacle. Another argument in favour of the CA having specialized functions was suggested by the results obtained using antiallatotropic substances in *Pheidole pallidula*. Precocene II prevents sexualization of the brood ; these results are similar to those obtained by Goewie et al. (1978) in *Apis* : the queen biased larvae which were treated with Precocene II develop into workerlike intermediates, following atrophy of the CA. Other less detailed results were obtained again in *Apis* by Dietz et al. (1979) : Precocene II in association with JH increased slightly the number of workers obtained (83 % as against 79 %) but the preparation was applied late after the orientation period.

Less is known about ecdysteroids because data is restricted to *Myrmica rubra* and *Pheidole pallidula* ; however the theory that they act in an opposite direction to JHA by favouring the production of workers, appears well-established. This being the case, in *Pheidole*, eggs rich in juvenile hormones

and poor in ecdysteroids give rise to worker larvae. A similar hypothesis based on the relative variations of JH and ecdysteroids has already been proposed for Termites by Lüscher (1976) and by Noirot (1979). Caste determination could therefore result from a succession of two series of factors ; first of all external factors related to the composition of the societies, to the quantity of available food and also the circulation of royal pheromones ; these external factors would have then as target the endocrine organs at the sensitive stage. These organs react by giving priority to either of the two antagonistic sets of hormones.

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EVOLUTION OF SOCIAL BEHAVIOURS

ALGUNAS CONSIDERACIONES SOBRE EL ORIGEN Y EVOLUCION DE LAS SOCIEDADES DE INSECTOS

A. de HARO

Departamento de Zoología, Universidad Autónoma de Barcelona, España

SUMMARY

Some considerations on the origin and evolution of insect societies

In Dictyoptera (Cryptocercidae) and Hymenoptera (Aculeata), we find anatomical and ethological characters preadapted for the exploitation of abundants resources with great carrying capacities : wood, nectar-polen and insects as prey for the larvae. The polygynic communal grouping by competitive – predatory pressions, favours the apparition of cohesive and cooperative characters which give more viscosity to the population in disminishing the cost paid to predators and construction of the nest. This grouping favours endogamy and development of genetic-like selection which fixes more and more cooperative characters in related polygynous groups. The existence in halictine bees of solitary and social species, show also the important question that, moreover the influence of phylogenetic pressions represented by preadapted characters, we must have in mind competition between the social populations and also the existence of surrounding pressions (carrying capacities of the trophic levels exploited and competitors-predators), in order to understand the origin and evolution of insect sociality.

El fenómeno social representa un nivel integrador más en la evolución animal, presentando interrelaciones individuales que obligan a tener en cuenta aspectos particulares y acumulativos en cuanto a los factores etológicos, genéticos y ecológicos que han participado en su origen y evolución.

Preadaptación

En los insectos encontramos dos grupos que poseen caracteres anatómicos y etológicos especiales, cuya explotación ha permitido, junto con otros factores, la diferenciación de la sociabilidad. Son los Dictyoptera a través de los Cryptocercidae y los Hymenoptera a través de los Aculeata. Ambos grupos poseen piezas bucales de tipo masticador aptas para el manejo de material de nidificación y alimenticio, estando preadaptados para la explotación de recursos abundantes y extendidos : la madera y el néctar-insectos como presas para sus larvas. Además los primeros son xilófagos, gregarios y lucífugos, mientras que los segundos son florícolas y depredadores, con el ovipositor transformado en aguijón como aparato de captura de presas para alimentar a su descendencia.

Wilson (1976), ve la preadaptación como una fuerza, en la historia de la especie, creadora de efectos multiplicadores. La preadaptación morfológica y conductal supone una presión filogenética, resultado de la historia de la especie, que orienta el sentido de la evolución como respuesta adaptativa a unas presiones ambientales. La explotación de recursos abundantes y estables, como la madera y el néctar-polen e insectos como presas, ha facilitado la estrategia demográfica de la K, apareciendo sociedades que tienen gran poder de acción ambiental a través de formas estériles y con pocos individuos reproductores, con ciclos largos de reproducción que tienden hacia una sola pareja en los Isoptera o a la monoginia en los Hymenoptera. Segun Michener (1964), hay relación inversa entre el tamaño del nido y la productividad media de las obreras (número de crias por obrera en un momento dado). En un nido monogínico, la productividad es mayor y ello produce una presión hacia la monoginia en condiciones estables ambientales. Junto con la monoginia evoluciona la conducta magnicida de la reina y obreras.

Los Vespidae sociales y los Formicidae, van a explotar originariamente los insectos como presas, mientras que los Apidae explotan el polen como fuente proteica. Los Isoptera han desarrollado la sociabilidad una vez, mientras que los Hymenoptera la han desarrollado independientemente como minimo 11 veces : dos en los Vespidae, uno en los Formicidae y ocho en los Apidae (Wilson, 1973).

Origen de la sociabilidad

En cuanto al origen de la sociabilidad, han de haber influido sobre los caracteres preadaptados, fenómenos de competición-depredación y la fácil accesibilidad de alimento. Las agrupaciones originarias han de ser de tipo poligínico comunitario, de acuerdo con Lin y Michener (1972), de individuos

no necesariamente emparentados estrechamente (Michener y Lange, 1958), cooperando en la construcción y defensa del nido, pero cuidando a su progenie por separado. La agrupación poligínica comunitaria (o de varias parejas en los termes), favorece la aparición de genes cohesivos y cooperativos que proporcionan, en términos de Hamilton (1964), mas viscosidad a la población, al disminuir, de acuerdo con Lin y Michener (1972), el coste pagado a los depredadores y el de la construcción del nido. Esta agrupación favorece la endogamia y el desarollo de la selección de semejantes genéticos, que cada vez fija mas los caracteres cooperativos en agrupaciones poligínicas emparentadas que alimentan las larvas en común.

En la selección de semejantes genéticos intervienen dos procesos : uno que tiende a unir los individuos por sus propiedades cohesivas y cooperativas, originando una selección de proximidad con otros indivuos del mismo grupo, mientras que el otro proceso une a los individuos por el sexo, originando una selección sexual. El primer proceso es el iniciador de las agrupaciones comunitarias favorecidas por las presiones de competición-depredación, encargándose el segundo de conferir mayor viscosidad a la población fijando los caracteres cohesivos y cooperativos. Los genes cooperativos producen el desarrollo del altruismo. Se produce tambien un sistema de dominación, origen de las castas, que produce la división del trabajo y el solapamiento con la descendencia adulta, originandose agrupaciones familiares poligínicas que constituyen la sociedad.

Estamos de acuerdo con West-Eberhard (1978) en que el origen de la sociedad de avispas es de tipo familiar poligínico, aunque pasando por las etapas previas antes expuestas. Los grupos poligínicos son comunes en abejas (Lin y Michener, 1972) y avispas (West-Eberhard, 1978). La vida subsocial o matrifilial (Wheeler, 1928) no parece ser el origen de la sociedad y de acuerdo con Lin y Michener (1972), hay relativamente pocos Himenópteros subsociales. Es la interacción madre-progenie la que ha desarrollado la sociabilidad, y este control materno (Alexander, 1974), creemos ha de ser posterior al control intergínico de castas que después se extiende a la descendencia al solaparse con ella, con dominación matrifilial. La selección familiar supone una capacidad de selección de semejantes genéticos, fijadora de los caracteres cooperativos. La confirmación de esta selección puede verse en el grupo de las seis semiespecies de *Drosophila paulistorum*, que se solapan más o menos. Según Lewontin (1974), las semiespecies no se diferencian morfologicamente, aunque ha habido diferenciación citológica y aislamiento reproductor, rehusando, en condiciones de laboratorio, las hembras de una semiespecie a los machos de la otra, aunque no tenga possibilidad de elección. Es un caso de selección sexual.

Las observaciones de Hay (1972) indican la capacidad de reconocimiento de individuos de *Drosophila* de los de otras cepas. Según Starr (1979), Kukuk et al. (1977), han proporcionado la evidencia indirecta de reconocimiento de parentesco por medio de olores en abejas Halictidae. En la selección de semejantes genéticos han de jugar también, entre otros, factores de impregnación química. Esta selección produce agrupaciones familiares originándose dentro de ellas la expansión de los genes altruistas debido a la eficacia proporcionada por los caracteres cooperativos en su explotación ambiental. Esta expansión de los caracteres sociales intragrupo familiar y de carácter selectivo individual, sera origen de una selección familiar en el sentido de Maynard Smith (1964). La selección familiar supone una selección individual, pues un individuo con mayor altruismo y por consiguiente con mayor capacidad de eficacia inclusiva, competirá favorablemente con otro con menor altruismo, adoptando también aquel estrategias etológicas especiales. La mayor eficacia inclusiva del altruista expande más su genoma.

Después se origina la selección de grupo, o interpoblacional, interdémica, en el sentido de Wilson (1976), originada por competición entre grupos no pertenecientes a la misma familia y poseedores de eficacia inclusiva diferencial.

Bases genéticas del fenómeno social

En cuanto a su base genética, la aparición del fenómeno social a partir de caracteres preadaptados, supone una recombinación favorecida por las presiones ambientales y productora de una presión filogenética dirigida en el sentido de explotar con más eficacia los recursos del ambiente. Los caracteres preadaptados suponen la existencia de gran variabilidad genética acumulada durante la filogenia del grupo en el depósito genético, creandose una presión filogenética que limita los cambios posibles en el genoma. De acuerdo con Ayala (1978), aunque la mutación sea la causa última de la variabilidad genética, constituye, no obstante, un suceso raro, suponiendo unicamente una gota de alelos nuevos en el depósito mucho más grande de la variabilidad genética almacenada. Esta variabilidad genética, proporcionará las nuevas recombinaciones que permitirán a la especie explotar las nuevas situaciones ambientales. Segun Lewontin (1974), la evidencia dice que los estadios iniciales de divergencia filética hacen uso de un repertorio ya existente de variación genética y si, de acuerdo con Lorenz (1965), todas las extructuras y funciones complejas de los cromósomas, con la mutación y la reproducción sexual, son un mecanismo creado al servicio de la función que consiste en adquirir y almacenar las informaciones sobre el ambiente, entonces el gran polimorfismo genético de las especies ha de representar el sedimento

filogenético de los cambios experimentados en las diversas líneas evolutivas a lo largo de la historia de la especie, o sea, el polimorfismo es una información almacenada y fuente para nuevas adaptaciones.

Nuevas recombinaciones génicas haran posible la aparición de caracteres cooperativos y la evolución de la sociabilidad, caracteres fijados por la selección de semejantes genéticos que pueden producir especiación simpátrida. Hay una tendencia general de los Himenópteros sociales de intercambiar individuos, como muestran por ejemplo las observaciones de Michener (1974), con datos de Sakagami y Hayashida (1968), con un intercambio entre nidos de *Lasioglossum duplex*, en que un 19 % de obreras de una población se unió a otra.

Evolución de la sociabilidad

En la evolución de la sociabilidad ha debido jugar un papel importante la agrupación familiar poligínica con solapamiento de la progenie adulta, al aumentar la eficacia inclusiva por incorporación de la descendencia al sistema intergínico de castas, con dominación materna. La fuerte endogamia durante el origen de la sociedad hace posible la expansión rapida de los genes cooperativos por la selección de semejantes genéticos. Ello corresponde a una fase inicial de contracción problacional debido a fenómenos de competición, depredación y facilitación de la actividad nidificadora, con aparición de los caracteres sociales eficaces en la explotación de los niveles tróficos. A esta fase de contracción inicial endogámica en que se fijan los caracteres sociales, sigue una fase de dispersión debido a fenómenos de competición intragrupo social, que será fuerte dada la semejanza genética existente. Cuestión esta que plantea un aspecto importante en la explicación del origen de la sociabilidad : el equilíbrio entre la necesaria endogamia para la fijación de caracteres, con la dispersion obligatoria que evite la pérdida de variabilidad genética y adaptación. La evolución de la sociabilidad se producirá explotando su depósito genético los nuevos grupos sociales, separados por su acción competitiva en el sentido de Wynne-Edwards (1962).

CONCLUSIONES

Los Dictyoptera (Cryptocercidae) y los Hymenoptera (Aculeata) tienen caracteres anatómicos y etológicos que les preadaptan para la vida social. Por presiones competitivas-depredadoras y facilitación en la construcción del nido, se forman grupos aislados en unos nichos ecológicos ricos en energia con gran capacidad de transporte (madera en los Cryptocercidae y

polen-nectar insectos como presas en los Hymenoptera Aculeata) y explotados de manera diferente. Estas agrupaciones poligínicas comunitarias disminuye el coste de la construcción del nido y el pagado a los depredadores, produciendose recombinaciones génicas que facilitan la cooperacion. Con ello se explota con mas eficacia el nicho ecologico segun la estrategia demografica de la K, provocandose una especiación simpátrida debido a la selección de semejantes genéticos que fija los nuevos caracteres cooperativos y altruistas aparecidos durante la explotación del nicho ecológico. Así se origina la sociabilidad.

El periodo de fuerte endogamia necesaria para el desarrollo de la cohesión social, es seguido por una fase de dispersión debido a competición intrafamiliar que permite la expansión de las nuevas sociedades. Entonces se origina la selección interfamilial, intergrupo o interpoblacional, que hará posible la explotación de los nuevos caracteres sociales y la evolución de los Isoptera e Hymenoptera sociales. La eficacia diferencial de grupos es el gran motor de la evolución. La importancia que tienen en la aparición y evolución del fenómeno social los niveles tróficos explotados y los factores biológicos competidores, queda reflejada en los termes y hormigas, formas edáficas, en que todos son sociales. Por el contrario, entre las avispas y abejas, formas aéreas, se encuentran especies solitarias. También la existencia en las abejas Halictinae de especies solitarias y especies sociales, plantea la interesante cuestión de que, además de la influencia de las presiones filogenéticas representadas por los caracteres preadaptados, se han de tener en cuenta la competición entre las mismas poblaciones sociales, asi como las presiones ambientales, para comprender el origen y evolución de la sociabilidad en los insectos.

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ECO-ETHOLOGY AND EVOLUTION OF SOCIAL SPIDERS

B. KRAFFT

Laboratoire de Biologie du Comportement, Université de Nancy I,
Case officielle n° 140, F-54037 Nancy Cedex France

SUMMARY

The various ways of social organization of spiders can be subdivided into four categories — territorial subsocial, non-territorial subsocial, territorial social, and non-territorial social. Familial behaviour seems to lie at the origin of these societies, at least in the species that weave irregular webs. The social spiders are distinguished from insect societies mainly by the spiders' use of their silk as a means of communication. The silk transmits various vibratory information enabling the individuals to coordinate their activities. Territoriality can be attributed to the geometrical structure of certain traps or to the necessity of maintaining a minimum capture area per individual. The evolution of spider societies can be attributed not only to minor ethological changes, such as the development of mutual tolerance, but also to particular ecological conditions.

RÉSUMÉ

Eco-éthologie et évolution des araignées sociales

Les différentes organisations sociales des Araignées se subdivisent en 4 catégories : les Araignées subsociales territoriales et non territoriales et les Araignées sociales territoriales ou non territoriales. Le comportement familial semble être à l'origine de ces sociétés, au moins chez les espèces qui tissent des toiles irrégulières. Les Araignées sociales se distinguent essentiellement des sociétés d'insectes par l'utilisation qu'elles font de la soie en tant que moyen de communication. Celle-ci transmet diverses informations vibratoires permettant la coordination des activités des individus. La territorialité peut s'expliquer par

la structure géométrique de certains pièges ou par la nécessité de maintenir une surface de toile de capture minimum par individu. L'évolution des sociétés d'Araignées s'expliquerait non seulement par des modifications éthologiques mineures, telles que le développement de la tolérance réciproque, mais également par des conditions écologiques particulières.

INTRODUCTION

The spiders, which are exclusively predatory arthropods, generally manifest strong intolerance towards their congeners. However, of the 30 000 species now known, about thirty show a more or less complex social organization (Burgess, 1978), by Wilson's definition of a society (1971) : «It is a group of individuals that belong to the same species and are organized in a cooperative manner». The organization of monospecific groups of spiders shows a gradation from solitary to social that makes it difficult to draw a clear and objective dividing line between these two ways of life (Krafft, 1979). Socialization has not produced morphological and physiological changes comparable with those in social insects. There are no castes, nor any obvious division of labour. The transition from solitary life to social life is made with a small number of behavioural modifications, such as the appearance of mutual tolerance and the exploitation of silky structures to transmit vibratory information (Krafft and Leborgne, 1979 ; Krafft, 1980). But «a small evolutionary change in the behavior pattern of individuals can be amplified into a major social effect by the expanding upward distribution of the effect into multiple facets of social life» (Wilson, 1975). The appearance of mutual tolerance, combined with favourable ecological conditions, has made possible the transition from a solitary status to a social one.

THE VARIOUS TYPES OF SOCIAL ORGANIZATION

The spiders that manifest a social organization can be subdivided, by reference to the structure of their groups and the nature of their webs, into four categories : territorial subsocial, non-territorial subsocial, territorial social, and non-territorial social.

Subsocial spiders

The species whose young cooperate, without intervention by the mother, for some time during the construction and maintenance of the nest or the capture of prey, but disperse before reaching adulthood, are known as

subsocial.This term suggests an evolution of the social phenomenon in accord with the most probable hypothesis on the origin of spider societies.

Territorial subsocial spiders : in this type of organization, still little studied, each individual exploits a portion of the web more or less exclusively. *Ixeuticus candidus* (Dictynidae, from Australia) weaves irregular webs. During the gregarious phase, the young construct their individual retreats in contact with the nest of the female (Main, 1971). *Eriophora bistriata* (Araneidae, from Paraguay) weaves orb webs. By day all the spiders cluster tightly against one another. At dusk, each spider weaves an individual web hung from the long, common frame threads. In such a colony, hunting is normally an individual matter, but when the size of the prey exceeds that of the spider, two or three individuals sometimes cooperate to overcome the prey. The spiders disperse when they become adults (Fowler and Diehl, 1978).

Non-territorial subsocial spiders : this type of organization is observed only among the spiders that weave irregular webs. Among many species showing maternal behaviour, the gregarious life of the young continues after the death of the mother. Some tasks are carried out in common, such as the construction of the trap and the capture of prey. The interactions necessary for this cooperation imply the existence of mutual tolerance and of a mechanism temporarily preventing the dispersal of the individuals, with effects resembling those observed in social spiders. This subsocial organization persists for different times among different species of the same family. Among the Theridiidae. *Theridion impressum* shows a non-territorial subsocial organization that is very fleeting : the young disperse after the second moult that takes place outside the cocoon ; in *Theridion sisyphium* the dispersal happens only after the fourth moult (Kullmann, 1972) ; and the individuals of *Anelosimus studiosus* remain grouped and cooperate up to the subadult instar (Brach, 1977). The same pattern is observed in the Eresidae : the dispersal of the young appears after the fourth ou fifth moult in *Stegodyphus pacificus*, after the fifth in *Stegodyphus lineatus*, and after the sixth in *Eresus niger* (Kullmann et al., 1972 ; Kullmann and Zimmermann, 1975).

Social spiders

The species whose adults stay grouped and cooperate in the capture of prey or the construction of the silky structure of the colony are known as social spiders. In some cases the adults cooperate in the care of the young, but these young are always less developed than among the highly evolved social insects.

Territorial social spiders : these spiders live in colonies made up of individual webs linked to one another by the frame threads. These frame

threads, which are established in common, constitute a tie between the individuals and permit an exchange of vibratory information. The individual webs hold either a single spider or a group made up of one adult female, several young of various ages, and perhaps a male. Each web can be likened to a territory according to the definition of Wilson (1975), since it is «an area occupied more or less exclusively by an animal or a group of animals by means of repulsions through overt defense or advertissement». The territorial social spiders that weave irregular webs, which are the best known, are *Dictyna calcarata* and *Dictyna albopilosa*, from Mexico, and *Mallos trivittatus*, of the southwestern United States, belonging to the Dictynidae (Jackson, 1978a). *Mallos trivittatus* shows both a territorial social structure and to some extent a non-territorial subsocial structure. Each web holds one adult female and perhaps several young and a male. The same social organization has been seen in a theridiid spider from Gabon, *Achaearanea disparata* (Darchen and Ledoux, 1978 ; Darchen, personal communication).

All orb-weaving social spiders are territorial. The colonies, which can holp up to 350 individuals, consist of orb webs linked to one another by frame threads and each holding only one spider. Territorial behaviour is well developed and hunting is an individual matter. Spiders without webs cling to the frame threads. This type of organization is observed in *Cyrtophora citricola* (Araneidae, from Africa), *Cyrtophora moluccensis* (Araneidae, from New Guinea), *Metabus gravidus* (Araneidae, from Costa Rica), and *Uloborus republicanus* (Uloboridae, from South America). The territoriality of these species limits their social interactions, but this type of organization implies a certain form of cooperation during the establishment of the frame threads, frequent interchanges of information between the individuals, and a certain development of mutual tolerance (Krafft, 1979).

Non-territorial social spiders : all the non-territorial social spiders belong to families weaving irregular webs. This type of silky structure facilitates the inter-individual relations to the extent that one web can be exploited simultaneously by several individuals. It is in this group that one finds the most elaborate social organization (Krafft, 1979). Most activities are carried out in common. The spiders cooperate during the construction of the silky structure, combine their efforts when prey is captured, and may cooperate in the feeding of the young. The colonies of some species can contain more than a thousand individuals of both sexes and all ages. The spiders of this type belong to families including also species that show parental behaviour or sub-social organization. The best-known species are *Mallos gregalis*, from Mexico (Dictynidae) (Jackson, 1979 ; Burgess and Witt, 1976), *Stegodyphus sarasinorum*, from Afghanistan and India (Eresidae) (Kullmann et al., 1972) ; *Anelosimus eximius*, from Central America (Theridiidae) (Brach, 1975) ; and

Agelena consociata and *Agelena republicana*, from Gabon (Agelenidae) (Darchen, 1967). *Agelena consociata* displays interattraction and mutual tolerance ; cooperates in the construction of the trap, the capture of prey, and the feeding of the young ; and also shows a group effect (Krafft, 1971, 1975).

The classification of the various types of social organization in the spiders is different from that generally adopted for insects (Michener, 1969). In insects, the classification is mainly based on the appearance of castes and the development of brood care. In spiders, whose young are less strictly dependent on the adults, owing to their mode of development, the functioning of the society is more oriented towards the elaboration of a trap that permits the capture of prey. The silky structures assure the transmission of the information necessary for the coordination of the activities of the individuals. All members of the society, including the young, benefit directly or indirectly from the consequences of this coordination. The care of the young is no more developed among the social spiders than among the solidary spiders that show maternal behaviour.

CONSEQUENCES OF GROUP LIFE AMONG SPIDERS

It is often difficult to evaluate objectively the adaptive value of ethological characters. Such an analysis very often amounts to hypotheses, but in the case of spiders some of them are strengthened by facts.

Adaptative aspect of non-territorial social organization

All the individuals, adults and young, benefit from the nest's protection against bad weather and possible predators. In web-spinning spiders, the harvest of food is closely related to the efficiency of the silky trap. Owing to the cooperation of a large number of individuals, this trap can be remade rapidly after being destroyed. The coordination of the activities of the individuals allows social spiders to capture much larger prey than they would be likely to overcome as isolated individuals. The effects of this is to enlarge the range of prey.

Captured prey are consumed communally. Individuals that did not participate in the capture also take part in the meal. Since spiders'digestion is partly external, it is not impossible that the participation of several individuals in the meal helps to better digest the prey. In certain species, the adult females feed the young of the first instars by regurgitation (Kullmann, 1972). The females may also feed young that do not belong to their own brood. In all cases, the young can benefit from prey captured by any individual of the

colony. Their development therefore becomes independent of the survival of their mother. This eliminates the hazards of harvesting food that are faced by the young of solitary species.

Lastly, the simultaneous presence of males and females in one nest facilitates encounters between the sexes. It would be useless to try to rank the various characteristics according to their adaptive value. Overall, their effects become evident in two ways. Firstly, the social spiders constitute high concentrations of individuals in a limited space. A nest of *Agelena consociata* extending over 5 m^2 can hold 500 to 1000 individuals. Such a concentration is never observed among solitary spiders. Secondly, the social spiders survive even though they have much less reproductive potential than most solitary species. This relative lack of reproductive potential is proportional to the development of maternal, subsocial, and social behaviours. *Agelena labyrinthica*, a solitary species, lays about 150 eggs per cocoon ; *Coelotes terrestris* (Agelenidae), which shows maternal behaviour, lays only 50 ; and *Agelena consociata* lays only 10. In the Theridiidae, *Theridion impressum* lays 100 eggs per cocoon, *T. sisyphium* lays 50, *Anelosimus studiosus* 35 to 50, and *Anelosimus eximius* 20 to 25. In the Eresidae, *Stegodyphus pacificus* lays 450 eggs, *St. lineatus*, which is also a subsocial species, lays 110, and *St. sarasinorum* lays about 40. While the artificial aspect of such a comparison must be emphasized, since the differences between species could be not only ethological but also ecological, this nevertheless suggests a reduction of egg-laying that parallels the development of social organization. These results should be considered in relation to the protection from which the young benefit and their nutrition by the adults, which reduce mortality.

Adaptative aspect of territorial social organizations

Several observations indicate that territorial social organization also has several advantages. The presence of frame threads bearing the whole of the colony facilitates the construction of the individual webs of *Metabus gravidus*. On average, one spider needs 23 minutes to construct an orb web at the periphery of the colony, whereas at the center of the colony spiders have an adequate network of frame threads and take only 19 minutes to construct their webs (Buskirk, 1975a). The construction of large colonies increases overall the efficiency of capture in *Cyrtophora citricola* (Rypstra, 1979). On average, 30 % of the prey that strike the silky structure are captured by the spiders. But this efficiency varies from 10 % for small colonies, with 17 individuals, to 40 % for large colonies, with 350 individuals. In a large colony, a prey that escapes from one individual web has more chance of falling into a neighbouring web. The construction of vast colonies also allows

spiders to exploit very open sites through which flying insects pass (Lubin, 1974 ; Buskirk, 1975a ; Rypstra, 1979).

This increased efficiency of capture of prey can be related to the fact that the colonies of territorial social spiders constitute a substantial concentration of individuals in a limited space. In one biotope it has been observed that *Mallos niveus*, a solitary spider, was present at a concentration of 12 individuals per 100 m^2, whereas in a comparable area up to 10 000 individuals of *Mallos trivittatus* can be found (Jackson and Smith, 1978). The young are not fed by the adults, but they generally establish themselves in their colony of origin, taking advantage of the frame threads put up by the adults.

It is difficult to evaluate the protection against possible parasites that territorial social life affords. However, when a hymenopteran parasite flies through a colony of *Cyrtophora moluccensis*, some females grip their cocoons and shake them vigorously. They are then imitated by other spiders, behaviour which suggests that this may be an alarm system (Lubin, 1974). Finally as for the non-territorial social spiders, the presence of males and females in the colony decreases the risks run in the search for sexual partners.

Disadvantages of social life

The social life of spiders does not produce only advantages. By day, certain prey can detect and thereby avoid the imposing silky structures of the colonies. On average, 40 % of insects avoid the colonies of *Cyrtophora citricola* (Lubin, 1974). Owing to the high concentration of individuals in a limited space, the volume of hunting web per individual is smaller for social spiders than for solitary spiders. The capture web of *Mallos niveus* has an area of about 35 cm^2. It is 5 cm^2 per individual for *Mallos trivittatus* and about 2 à 3 cm^2 for *Mallos gregalis* (Jackson and Smith, 1978). This reduction of the capture area per indivual can be partially compensated for by an increase in the capture rate, that is, the percentage of prey touching the web that is captured. But such a balance can be reached only in favourable ecological conditions. Indeed, non-territorial social species are found only in the tropical regions. It seems that the social spiders have been able to develop only in biotopes that permanently contain a high enough density of prey.

TERRITORIALITY AND SOCIAL ORGANIZATION

The amount of prey captured depends on many factors, including the area of the trap and the web-site selected by the spider. Because insects are

distributed heterogeneously in the biotope, not all web-sites are equivalent (Pasquet and Krafft, 1980). Selection of the most favourable sites involves intra-specific competition (Riechert, 1976). In the solitary spider *Agelenopsis aperta*, each individual occupies a hunting space whose dimensions, which greatly exceed the area of the web, are inversely proportional to the density of prey. This hunting space can range from 0.10 to 10 m^2. When, in any given biotope, two spiders exploit an area equivalent to one individual hunting space, the capture rate for each individual is reduced by 40 % (Riechert, 1978a, 1978b). The agonistic behaviour of these spiders therefore has the effect of balancing their energy budgets. The young of *Tegenaria domestica*, which are raised in groups, show in the laboratory a cannibalism that is inversely proportional to the amount of prey given to them (Mielle, 1978). Solitary *Amaurobius* or *Stegodyphus* species can be kept so close together in one enclosure that their webs touch, on condition that enough prey is distributed to them. In the colonies of *Metabus gravidus*, the individuals that have orb webs manifest agonistic behaviour when a congener approaches. These displays of aggressiveness are no longer observed when the spiders are situated on the frame threads (Buskirk, 1975). The colonies of *Cyrtophora citricola* are made up of several concentric layers of individual webs. The intermediate layers have the highest rates of capture – and it is in these most efficient layers that the spiders most often manifest agonistic interactions (Rypstra, 1979).

These various observations suggest that the territorial behaviour of the spiders corresponds to the defense of a hunting space big enough to ensure that each individual's energy budget is balanced, in accord with the ecological conditions, that is, the density of prey. Finally, it must be emphasized that the orb web of the orb-weaving spiders, because of its structure, cannot be exploited efficiently by several individuals simultaneously. These facts undoubtedly explain the existence of territorial social spiders and the dispersal of subsocial spiders. As they develop, the young of subsocial species have increasing energy needs. The web gradually becomes unable to provide for the needs of all the individuals, resulting in the appearance of agonistic behaviours, which are responsible for the dispersal. This hypothesis seems to be confirmed by the fact that in the laboratory the disappearance of mutual tolerance and of the grouping tendency in *Coelotes terrestris* can be delayed by feeding the young generously (Horel et al., 1979). Theoretically, the spiders would be able to choose to increase the dimensions of their trap. But such an extension is rapidly limited by the damping of the vibratory phenomena transmitted by the web. At too great a distance a prey might not be detected. The dispersal can be total, or, on the contrary, limited, as is the case for *Mallos trivittatus* or *Achaearanea disparata*. The territoriality of the territorial social species would

have the effect of ensuring a minimum capture area per individual compatible with their energy needs, while preserving a high efficiency for the trap which the colony represents. In biotopes rich in prey, territoriality has disappeared in certain species, thus giving rise to the non-territorial social spiders. Certainly it is possible to find in one biotope non-territorial social, territorial social, and solitary species. They may be species belonging to different families, exploiting different microhabitats, with capture techniques that are not necessarily equally efficient. But on the other hand territoriality must be considered an adaptive factor that has undergone strong selective pressure among the solitary spiders. Such characters are liable to be maintained, even in ecological conditions that could conceivably allow them to disappear.

This hypothesis is also reinforced by the existence of temporary aggregations of solitary spiders in favourable ecological conditions. In *Leucauge* species from Costa Rica, 50 % of the adults are gregarious. These aggregations hold from two to eleven individuals, whose webs are linked to one another (Valerio and Herrero, 1977). Depending on the ecological conditions, the individuals of *Philoponella semiplumosa* (Uloboridae, from Costa Rica) are gregarious or isolated. The associations are temporary and facultative (Lahmann and Eberhard, 1979). The same is true for *Nephila clavipes* (Farr, 1977). Therefore there is a possibility of temporary, facultative gregariousness among adult spiders according to the conditions of the biotope. The presence of many prey would produce a reduction of the territoriality, allowing the webs to be close together.

CONCLUSION

The comparison of these different types of social organization makes it possible to give a picture of the stages that have led from the solitary to the social spiders.

In the non-territorial social spiders, which all weave irregular webs, association seems to have originated from species displaying maternal behaviour. The appearance of cooperation among the young led to the subsocial species. Favourable ecological conditions made possible the transition to the social type of organization, since the young no longer found it necessary to disperse in order to satisfy their energy needs. In all the families concerned, in fact, there are solitary species, species that display maternal behaviour, subsocial species in which the dispersal of the young comes more or less late, even as late as the subadult instar, and finally social species (Krafft, 1979). This evolution has apparently been able to occur only in regions with ecologically favourable conditions.

To be clearly established, the evolution of territorial social species still requires further investigation. For the spiders that have irregular webs, however, it may be assumed that the young which disperse, either immediately or after staying for some time in their mother's web, stay in the immediate vicinity, exploiting in part the pre-existing frame threads. This partial dispersal might be the consequence of ecological conditions that have not induced a complete disappearance of territorial behaviour. Unfortunately, we have no data about the maternal behaviour in these species.

The path towards socialization has been blocked among the orbweaving spiders by the geometrical structure of their webs. The species do not display any elaborate maternal behaviour. Because the young do not systematically disperse they weave their webs in contact with that of their mother, or within the colony when this already exists. The hypothesis of the assembly of adults under the influence of favourable ecological conditions, combined with the absence of dispersal of the young, must still not be set aside. But regardless of the ecological conditions, none of these species has reached the stage of adopting a non-territorial social organization. The important role that ecological factors seem to have played in the appearance of spider societies can be explained by the fact that socialization in these animals has not necessitated morphological changes and depends on a very few ethological changes, such as the absence of dispersal and the appearance of mutual tolerance. The presence of silky structures has doubtless been a determining factor, constituting a particularly efficient means of communication between individuals (Witt, 1975).

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EVOLUTION OF CHEMICAL DEFENSES IN TERMITES

G. PRESTWICH

Department of Chemistry and Program of Ecology and Evolution
State University of New York, Stony Brook, N.Y., 11794 U.S.A.

SUMMARY

The discovery of novel diterpenes in the soldier frontal gland secretions of higher termites has led us to detailed biochemical, and ecological investigations into the evolutionary and biosynthetic origins of defense compounds in termite societies. (1) Termitine soldiers often possess both mechanical and chemical defenses (e.g., *Cubitermes*) based on greasy diterpene hydrocarbons of both irregular and regular terpenoid structures. (2) Nasute termites (e.g., *Nasutitermes*) squirt a terpenoid glue, containing unique tetracyclic and tricyclic diterpenes. New structures, a physiocochemical model for the glue's stickiness, biosynthetic studies, and the use of secretion compositions as clues to termite phylogeny are discussed. (3) Advanced rhinotermitids (e.g., *Prorhinotermes, Schedorhinotermes* and *Rhinotermes*) employ electrophilic lipids (vinyl ketones, nitroolefins, β-ketoaldehydes) as contact poisons. Prevention of auto-intoxication may operate in this subfamily, furnishing evidence for a ancestral insecticide detoxication system.

RESUMEN

Evolución de las defensas químicas en las termitas

El descubrimiento de diterpenos nuevos en las secreciones de la glándula anterior de los termites soldados avanzados nos ha guido a investigaciones detalladas bioquímicas y ecológicas de los orígenes evolutivos y biosintéticos de compuestos defensivos en las sociedades de termitas. (1) Los termites soldatos frecuentemente tienen defensas mecánicas y químicas (por ejemplo, *Cubitermes*) basadas en hidrocarburos diterpenos grasosos de

estructuras irregulares y regulares. (2) Los termites nasutes (por ejemplo, *Nasutitermes*) arrojan una goma terpénica, que contiene diterpenos tetracíclicos y triciclicos únicos. Nuevas estructuras, un modelo fisioquímico para la tenacidad de la goma, estudios biosintéticos, y el uso de compuestos de secreciones como guias hacia la evolucion de los comejenes son examinados. (3) Los Rhinotermitidos avanzados (por ejemplo, *Prorhinotermes, Schedorhinotermes* y *Rhinotermes*) usan lípidos electrofílicos como venenos de contacto. La prevención de auto-toxicación puede operar en esta subfamilia, mostrando evidencia para un sistema ancestral de desintoxicación contra insecticidas.

INTRODUCTION

We have been involved for the past five years in the detailed study of chemical defense by termite soldiers, in particular with respect to (1) structure determinations of new chemical substances, (2) elucidation of biosynthetic pathways, (3) biochemical mechanisms of detoxication, (4) inter- and intra-specific chemical variation, and (5) application of chemosystematic characters to concepts of termite evolution. In addition, we are involved in the design of metabolism-activated, delayed-action toxins for selective control of social insects which have been designated as pests. In this paper, I will present first an overview of our work with termite chemical defense by highlighting some of our recent results. Chemical defense in Isoptera has independently evolved numerous times in the families Rhinotermitidae and in the Termitidae (Fig. 1). Quennedy (1975) has classified these mechanisms as (1) biting, with the injection of an irritant as in the Termitinae and Macrotermitinae (or antihealant, cf. Prestwich, 1979a), (2) labral brushing, with the topical application of a contact insecticide as in Rhinotermitinae, (3) squirting, with the ejection of a viscous terpenoid glue, as in the Nasutiterminitinae. The chemistry of these techniques has been reviewed (Prestwich 1979a, b, c). This paper will focus on the following recent discoveries in the poison-brushers and glue-squirters :

1 Rhinotermitinae (poison-brushers)
   a. New Chemicals
   b. Biosynthetic Pathways
   c. Detoxication
   d. Phylogenetic Interpretations

2 Nasutitermitinae (glue-squirters)
   a. New Chemicals
   b.Chemosystematic Analyses
   c. Biosynthetic Pathways
   d. Phyletic Interpretation

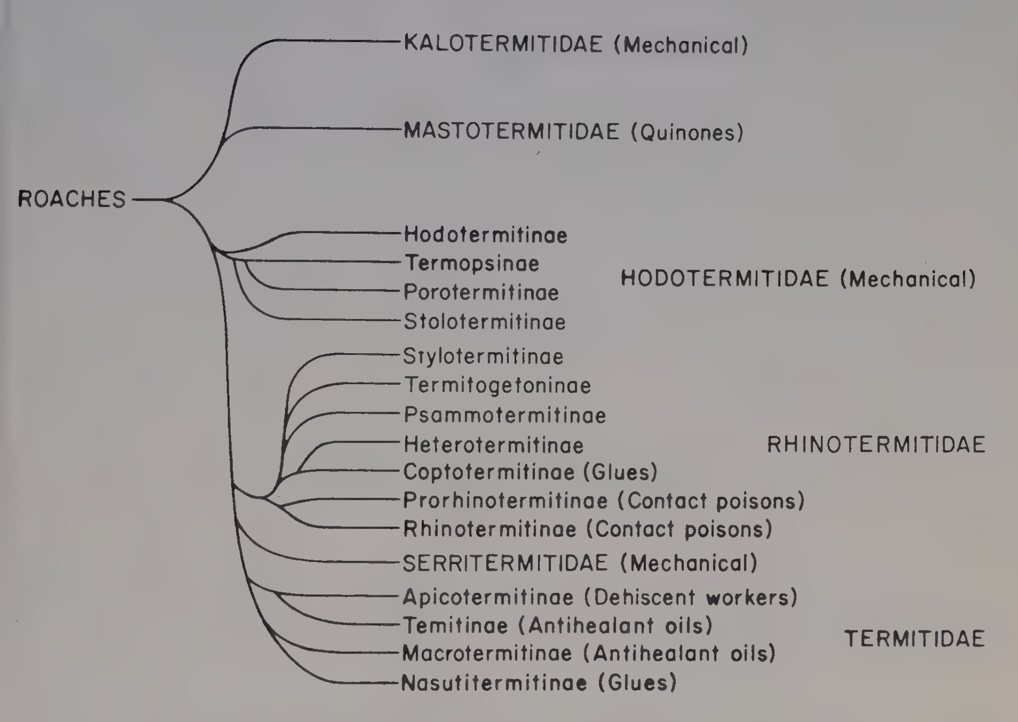


Fig. 1 – Phylogeny of Isoptera, with regard to evolution of chemical defense

Fig. 1 – Filogenia de los Isópteros, con referencia a la evolución de la defensa química

RHINOTERMITINAE

The monomorphic soldiers of *Prorhinotermes simplex* (subfamily Prorhinotermitinae) produce a cephalic defense secretion which is > 90 % of a single nitroolefin, 3, (Vrkoč and Ubik, 1974). Major and minor soldiers of the termites *Schedorhinotermes putorius* (Quennedy et al., 1973) and *S. lamanianus* (Prestwich et al., 1975) produce up to 35 % of their dry weight as a mixture of 3-alkanones, l-alken-3-ones (1) and α, ω-alkadien,3-ones (2) which act as contact poisons to attacking ants. Recently, we have found that the most advanced genera of this subfamily, *Rhinotermes* and *Acorhinotermes* produce β-ketoaldehydes, a hitherto unknown class of naturally-occuring defense chemicals. These contact poisons – the nitroolefins, the vinyl ketones,

1, n= 7,9,11 — 2, n= 7,9,11 — 3 — 4, n= 9,11,13 — 5

6 — 7a — 7b

8 — 9

Fig. 2 – Rhinotermitine defense secretions

Fig. 2 – Las secreciones defensivas de los Rhinotermitinos

and the β-ketoaldehydes – are all highly reactive electrophilic agents in terms of their abilities to alkylate biologically important nucleophilic sites (-OH, -SH, $-NH_2$ groups). Rhinotermitine defense chemicals are shown in Fig. 2.

The C_{14} β-ketoaldehydes 6 and 7 were isolated as > 80 % of the crude hexane extract of the «nasutoid» minor soldiers of the neotropical species *Rhinotermes hispidus* and *R. marginalis* (Prestwich and Collins, 1980). The corresponding C_{13} 2-alkanones 4 and 5 were also isolated, suggesting that the β-ketoaldehydes arise from reductive cleavage of a β-ketofattyacyl-CoA derivatives which are normally involved in the energy-releasing β-oxidation pathway for fatty acids. In the major soldiers, however, these compounds were completely absent ; this contrasts with the more primitive *Schedorhinotermes* spp., in which major and minor soldiers have identical and abundant chemical defenses. The Guyanese termite *Acorhinotermes subfusciceps* has undergone a secondary loss of the major soldier caste, and thus has only nasutoid minor soldiers. Hexane extracts of the soldiers give the sixteen-carbon β-ketoaldehyde 9 as the major product and *ca.* 5 % of the Z-8-pentadecen-2-one (8) as the minor product (Prestwich and Collins, 1981b). The compounds can be formally derived from reductive cleavage of the β-ketopalmitoleoyl-CoA as described above. This would appear to be an extraordinarily parsimonious biochemical means for defense substance production ; i.e., the

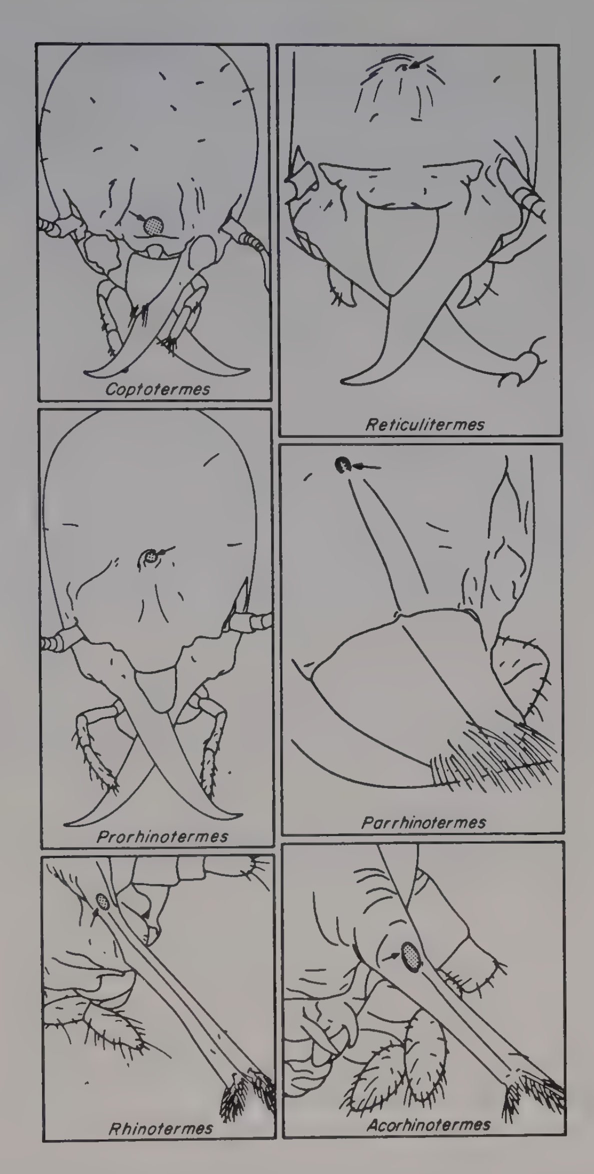


Fig. 3 – Morphological trends in the evolution of the frontal weapon of Rhinotermitidae (redrawn from Quennedey and Deligne, 1975)

Fig. 3 – Tendencias morfológicas en la evolución del arma frontal de los Rhinotermitidae

fatty acid degradation enzymes have been harnessed to provide lipid-like contact poisons. The morphological trend in this subfamily is the regression of the mandibles with the prolongation of the labrum into a daubing brush (Quennedey and Deligne, 1975). (Fig. 3). The mandibulate major soldier caste decreases in numbers and chemical weaponry until it is eventually lost in *Acorhinotermes*. The chemical instability and thus inherent reactivity of the defense chemical which the nasutoid minor soldiers deploy increases with evolutionary advancement. Finally, it appears that selection favors the minimum amount of additional enzymic machinery to carry out the preparation of the defensive chemicals. As a result, the more advanced termites employ chemicals which are structurally more similar to normal intermediates in fat metabolism.

The increasing toxicity of chemical weapons also demands increased ability to autodetoxify these metabolic poisons. Using ^{14}C-labelled defense secretions of *P. simplex* and *S. lamanianus*, we have now established that workers of these termite species possess substrate specific detoxication pathways which convert the lipid-soluble defense compounds of conspecific soldiers into less reactive, double bond reduced forms (Spanton and Prestwich, 1981). One of these detoxication systems, that of *P. simplex* may also involve a glutathione S-transferase enzyme which converts the nitro-olefin 3 by a Michael-type addition reaction to the glutathione conjugate. Simple log dose-survival experiments have been performed to compare mortality in *P. simplex, S. lamanianus*, and the non-adapted species *Reticulitermes flavipes*. Worker survival for the *S. lamanianus* soldier vinyl ketone is *S. lamanianus* > *P. simplex* > *R. flavipes* ; however, worker survival in the presence of the *P. simplex* nitro-olefin decreases in the order *P. simplex* > *S. lamanianus* > *R. flavipes* (Spanton and Prestwich, 1981).

NASUTITERMINAE

The soldiers of the advanced genera of this subfamily possess an elongate rostra, called the nasus, which is used to eject a viscous and sticky terpenoid secretion. These secretions are sticky because they contain high concentrations of hydrogen-bonded, dome-shaped diterpenes in a monoterpene solvent (Prestwich, 1979b). The structures of the tricyclic trinervitanes (10) (Prestwich et al., 1976), tetracyclic kempanes (11) (Prestwich et al., 1977) inspired further investigations into their biosynthetic origins and further searches for biosynthetic key intermediates (Prestwich, 1979a, c). Recent discovery of bicyclic secotrinervitanes in *Nasutitermes* (Braekman et al., 1980) and *Longipeditermes* (Prestwich, Goh, and Tho, unpublished) provide

14, $R_1 = R_2 = R_3 = C_2H_5CO$

Fig. 4 – Structures of diterpenes from Nasutitermitinae

Fig. 4 – Estructuras de los diterpenos de Nasutitermitinae

further evidence for a stepwise progression from the monocyclic fourteen-menbered ring cembrene-A to bicyclic, tricyclic, and tetracyclic carbon skeletons. The correct cembrene-like arrangement of carbon atoms in space is preserved in the bicyclic compounds and in a new tricyclic tripropionate (14) (Prestwich et al., 1981a). Furthermore, alternate ring-forming pathways may occur in the tricyclic to tetracyclic conversion, as shown by the existence of the 1,2-methyl shifted skeleton of the rippertanes (13) (Prestwich et al., 1980a). Unique functionalization of the tetracyclic kempane skeleton (12) occurs in *Nasutitermes octopilis* from Guyana (Prestwich et al., 1979), and this may provide an adaptive edge in survival in woody litter relative to sympatriç arboreal *Nasutitermes* species (Collins and Prestwich, 1982). These different diterpenes are shown in Fig. 4.

Intraspecific variation of defense chemicals in isolated populations of *Trivervitermes gratiosus* (Prestwich, 1978), and *T. bettonianus* (Prestwich and Chen, 1981) give rise to genetically distinct chemical «races». The chemical

Fig. 5 – Biosynthetic pathway for nasute diterpenes, showing the incorporation of 2-^{14}C-mevalonolactone into geranylgeranyl pyrophosphate, cembrene-A, and then into trinervitanes and kempanes.

Fig. 5 – Via biosintética de los diterpenos de nasutes, mostrando la incorporación de 2-^{14}C mevalonolactona en el geranilgeranil pirofósfato, cembreno-A, y después en los trinervitanos y kempanos

composition of the soldier secretion was shown to be invariant under conditions in which field-collected alates were raised to incipient colony status in the laboratory and fed grass from the region of a different *T. bettonianus* chemotype. This was also taken as further evidence for the *de novo* biosynthetic origin of these secretions in the soldier frontal glands.

Biosynthesis (Fig. 5) was unambiguously demonstrated by injection of ^{14}C-labelled acetate and mevalonate derivatives into the abdomens of *N. octopilis* soldiers using microcapillary techniques (Prestwich, Jones and Collins, 1981b). After 12-24 hr, soldiers were decapitated and 2-5% of the radioisotopic label was recovered from the hexane-soluble material in the soldier's head. Purified mono- and diterpenes showed .05-0.3 % incorporation of label, indicating relatively rapid and efficient incorporation of the precursors.

Chemical investigations of the frontal gland secretions of three *Subulitermes* spp. from Guyana reveal the presence of sesquiterpenes neo-intermediol and T-cadinol and tricyclic diterpenes identical to the trinervitanes found in several neotropical *Nasutitermes* species (Prestwich and Collins, 1981a). Thus, identical diterpenes occur in advanced nasutes at the distal ends of both alleged phlyetic lines as originally proposed by Emerson (1961). In view of the absence of diterpenes in the primitives manidibulate nasutes *Syntermes, Cornitermes, Armitermes*, and *Rhynchotermes*, we have suggested that the diphyletic hypothesis for the origins of Nasutitermitinae is probably no

longer tenable. An alternate monophyletic route (Fig. 6) is proposed in which all glue-squirting, non-mandibulate nasutes are derived from a common ancestor which probably evolved prior to the separation of West Gondwana into proto-Africa and proto-South America in the Cretaceous.

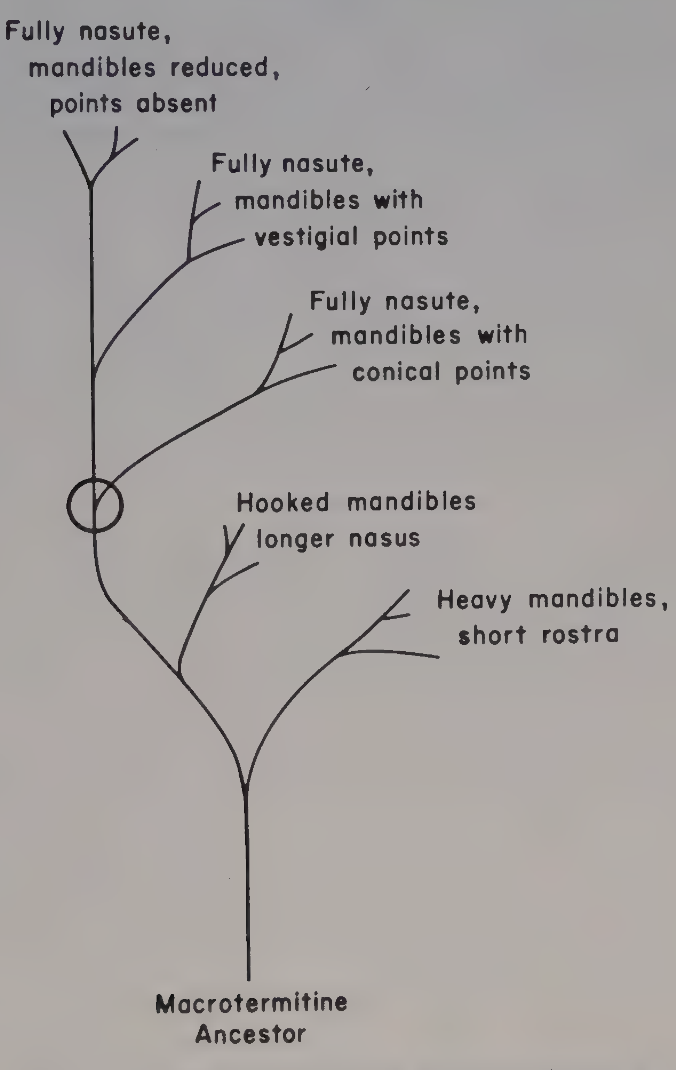


Fig. 6 – Proposed monophyletic origin for glue-squirting nasutes

Fig. 6 – Origen monofiletico propuesto para los nasutes que proyectan goma

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THE NATURE AND EVOLUTION OF SWARMING IN TROPICAL SOCIAL WASPS (VESPIDAE, POLISTINAE, POLYBIINI)

M.J. WEST-EBERHARD

Smithsonian Tropical Research Institute, Balboa, Panamá
(Mail : Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica, Central América)

SUMMARY

Absconding (evacuating) swarms of social wasps following damage to nest or brood are more likely when the brood is young. Reproductive (fissioning) swarms in *Metapolybia aztecoides* occur during periods of much competition among queens. When a well-developed queen or group of queens is present nest enlargement rather than swarming may follow peaks of female production. In times of worker shortage neither nest enlargement nor swarming occurs. Seasonal swarming is reported in some species from 5° - 20° N. latitude, and from 12° - 35° S. latitude. Preparations for swarming include regrouping, cessation of nest building, unusual readiness to fly when disturbed, buzzing runs, trail marking, and, sometimes, brood cannibalism, aggressive begging, new nest initiation, and temporary aggregation along the swarm route. Old workers serve as scouts. Swarming individuals independently search for scent marks, with efficiency probably improved by use of prominent landmarks, conservation of direction and altitude between marks, and close spacing of marks at turns. Two possibly intergrading modes of trail following distinguish «diffuse» and «clumped» swarms. The trail pheromone is probably derived from sternal gland secretions originally important in dominance and territoriality, and subsequently used as «assembly» pheromones, orientation cues, recruitment signals, and (finally) markers guiding long migrations. There may be some co-evolution of pheromonal trail marking by swarming females and that of conspecific males. Honeybee swarming, like wasp swarming, is associated with periods of marked intracolony reproductive competition, whose onset is timed via regulation of queen rearing.

RESUMEN

La naturaleza y evolución del enjambrazón en las avispas sociales (Vespidae, Polistinae, Polybiini)

En las avispas sociales los enjambres de abandono del nido después de algún daño al nido o a su cría son más frecuentes cuando la cría está joven. Los enjambres reproductivos (fisión de la colonia) en *Metapolybia aztecoides* ocurren cuando haya much a competencia entre las reinas. En el caso que hayan presentes una o varias reinas bien desarolladas, la extensión del nido en vez de la enjambrazón puede seguir la producción de un grupo grande de hembras adultas. Durante las épocas de escasez de obreras no ocurre ni formación de enjambres ni extensión del nido. Enjambres estacionales se han descrito en algunas especies entre las latitudes 5° N. y 20° N., y 12° S. y 35° S. Los preparativos para enjambrar incluyen reagrupamiento sobre o cerca del nido ; paro de construcción ; tendencia al vuelo con poco estímulo ; carreras cortas y rápidas sobre el nido ; establecimiento de un camino marcado con feromonas ; y, a veces, canibalismo de la cría, solicitación agresiva de alimentos, comienzo de construcción del nido nuevo, y agrupación en la ruta establecida para guiar el enjambre. Las obreras viejas toman el papel de guias. Cada individuo sigue la ruta buscando las pistas químicas, con mejor resultado por el uso de puntos sobresalientes, por conservar la misma altura y el mismo sentido entre puntos marcados, y por la aplicación de marcas adicionales donde voltea la ruta. Existen dos modos de seguir la ruta (con posibles formas intermedias) : enjambres difusos, y enjambres agrupados. La feromona utilizada para guiar enjambres es probablemente derivada de sustancias producidas por glándulas esternales originalmente importantes en comportamiento de dominancia y territorio, y después usadas como feromonas de agrupamiento, como pistas de orientación, como atrayentes a nidos nuevos, y, finalmente, para marcar la ruta de migraciones largas. Puede haber co-evolución de feromonas de enjambrar con las usadas por machos de las mismas especies para marcar rutas de patrullaje. Los enjambres de abejas son en muchos detalles semejantes a los de avispas, siendo también asociados con competencia reproductiva marcada, cuyo comienzo se coordina por regular la producción de reinas.

INTRODUCTION

One of the most distinctive behavioral characteristics of the large-colony tropical social polybiine wasps is the ability to found nests by swarming. That is, movements between old and new nest sites are effected by the coordinated synchronous migration of large numbers of individuals including both workers and queens. Among the social insects only the tropical polybiine wasps and the highly eusocial bees (*Apis* species and stingless bees,

Meliponini) are said to swarm, although the fissioning and migration of certain ant colonies (e.g., army ants) are parallel phenomena. Among the 35 currently recognized genera of social wasps (see Richards, 1978) all except seven are known or believed likely (as Polybiini) to found nests in swarms. The seven non-swarming genera include the Vespinae (yellow jackets and hornets), *Polistes*, and four primarily tropical Polybiine genera similar to *Polistes* in usually building unenveloped combs : *Ropalidia, Parapolybia* and *Belonogaster* in the Old World ; and the primarily neotropical genus *Mischocyttarus*. In these genera nests are sometimes initiated by groups of females which, especially if a former nest was located near the site, may be quite large and loosely referred to as a «swarm» (see below). However, there is so far no unequivocal evidence for swarming (synchronous, coordinated migration) in any of these «non-swarming» genera.

The swarming behavior of wasps has only recently attracted the attention of investigators. Naumann (1975) was the first to describe the abdominal «dragging» behavior along the route followed by swarms, and Jeanne (1975a, 1981) has experimentally confirmed Naumann's conclusion that the swarming wasps follow a scent trail made by applying the secretion of an abdominal gland to «dragged» (rubbed) surfaces. Two kinds of swarms have long been distinguished (e.g., see Richards and Richards, 1951) : *absconding* (secondary, or evacuating) swarms, produced when the nest is abandoned following some catastrophe (such as predation or other damage to the nest) ; and *reproductive* (primary, or fissioning) swarms, produced when a part of the adult population of a colony leaves to begin a new nest. Although the two kinds of swarming entail much similar behavior (e.g., chemical trail marking by scouts, and coordinated leaving of the original site), there may be important differences between them (e.g., with regard to migration distance, preparations for swarming, and swarm composition). The majority of observations so far available deal with either induced or naturally absconding swarms, or with migrating or recently settled swarms of unknown origin. *Seasonal* swarms occur in some species, and can involve both absconding (nest abondonment) (see Naumann, 1970) and budding (departure of only a portion of the colony adults) (Richards, 1978, after Rodrigues, 1968).

This report is based on the few published reports of swarms and swarming behavior, as well as on my own observations of swarming and related biology in 15 Polybiine species (Table I).

Table I – Species observed, and localities

Tabla I – Especies observadas y localidades

Species	Locality
Brachygastra augusti (de Saussure)	Cali, Colombia
Leipomeles dorsata (F.)	Panama, Barro Colorado Island
Metapolybia aztecoides Richards *	Cali, Colombia
Parachartergus apicalis (F.) *	Near San Jose, Costa Rica
Parachartergus colobopterus (Lichtenstein)	Gaira, Madgalena, Colombia
Polybia diguetana R. du Buysson	San Antonio de Escazu, Costa Rica
Polybia ignobilis (Haliday)*	Cali, Colombia
Polybia liliacea (F.)	Puerto Viejo, Meta, Colombia
Polybia raui raui Bequaert*	San Antonio de Escazu, Costa Rica, & Chiriqui, Panama
Polybia scrobalis pronotalis Richards	Cali, Colombia
Polybia sericea (Olivier)	Puerto Viejo, Meta, Colombia
Stelopolybia areata (Say) *	San Antonio de Escazu, Costa Rica
Stelopolybia hamiltoni Richards *	San Antonio de Escazu, Costa Rica
Synoeca surinama (L.) *	Puerto Viejo, Meta, Columbia

* Species in which swarm movement observed by the author. Colonies of other species listed observed either while preparing to swarm, after nest initiation, or performing other swarm-related behavior in the text. Specimens identified by O.W. Richards and deposited in the British Museum of Natural History, London.

* Especies en las cuales el autor observó el movimiento de enjambrazón. Colonias de las otras especies citadas observadas ya sea cuando se preparaban a enjambrar, despuès de la iniciación del nido, o desarollando comportamiento discutido en el texto.

THE DECISION TO SWARM : CONDITIONS PRECEDING SWARMING

Absconding swarms, with nest abandonment, can follow a variety of kinds of catastrophes which befall colonies. Those observed include predation by army ants (Richards and Richards, 1951 ; Naumann, 1975 ; Chadab, 1979, pers. obs. of *Metapolybia aztecoides*) ; predation by animals capable of damaging the nest envelope (e.g. bats : Jeanne, 1970 ; pers. obs. of damage by an unknown predator of *Synoeca surinama* in Meta, Colombia) ; invasion by insect parasitoids (e.g., phorid filies – see Schremmer, 1972) ; overheating (pers. obs. of *Metapolybia aztecoides*) ; severe damage to a nest due to a landslide provoked by heavy rainfall (pers. obs. of *Polybia raui*) ; etc. A recently abandoned nest of *Polybia liliacea* contained termites in the nest carton near its attachment to the supporting branch and no other obvious sign of damage or predation. In short, many kinds of damage are associated with nest abandonment. But little is known about how the wasps decide to migrate rather than wait or repair damage. Evidently the odor (or presence of only a few individuals) of army ants is sometimes sufficient to induce nest abandonment (Chadab, 1979). On the other, Jeanne (1970) observed that

large colonies of *Polybia sericea* would calmly repair damage by predatory bats, abandoning the nest only when attacked on more than one successive night. I have repeatedly removed large sections of nest envelope from observation nests of *Metapolybia* and *Synoeca* without provoking swarming. One variable which seems to affect readiness to abscond is the composition of the brood. I have noticed that colonies with few pupae and large larvae (a large proportion of eggs and small larvae) seem more likely to abandon manipulated nests. For example, the sudden shining of bright light for only a few seconds on a newly founded comb of *Synoeca surinama* caused the wasps to immediately stop building and begin swarm preparations. They abandoned the nest (which contained eggs and a half-completed envelope) two days later. Chadab (1979) also noted an unusual readiness to abscond in an *Apoica* colony whose brood consisted primarily of eggs in recently vacated cells. Forsyth (1978) documented this tendency in a study of *Metapolybia azteca* in Costa Rica : seven of 41 colonies absconded within a day after the capture of all adults for marking and subsequent release. All seven nests contained few or no larvae, although the colonies were in different stages of development (three were newly founded ; three were mature, male-producing colonies ; and one lacked brood following dry-season cannibalism). This effect of brood composition on readiness to swarm makes sense in terms of natural selection : there is less to be gained by short-term adherence to a nest which is empty or contains only brood which would require many days to rear, whereas staying with a large nearly mature brood for even a day might pay off in the form of many additional young adults. Furthermore, the presence of only very young brood or many empty cells often reflects reproductive periodicity which can affect the advantage of swarming in other ways : a young brood often follows a large emergence of adults, and the presence of a large proportion of young individuals in a swarm enhances the likelihood that it will survive the long period (4-6 weeks) before additional workers can be produced. High worker mortality often produces a crisis during this period (see West-Eberhard, 1981), and repeated absconding at short intervals (or just preceding a large emergence of adults when reproduction is pulsed) could lead to colony extinction. It is therefore of interest that Naumann (1970) observed what he believes to be «enforced» reproductive periodicity in seasonally swarming tropical species, with adults cannibalizing intermediate-aged brood so that imagoes are produced synchronously. Swarms then follow soon after large emergences.

Reproductive swarming conditions are difficult to document, because it is difficult to predict when colony fission is likely to occur. Even in seasonally swarming species, not all colonies produce swarms, and knowing that a swarm has departed requires either direct observation, or extensive marking and censusing of individuals. Seasonal reproductive swarming in *Metapolybia*

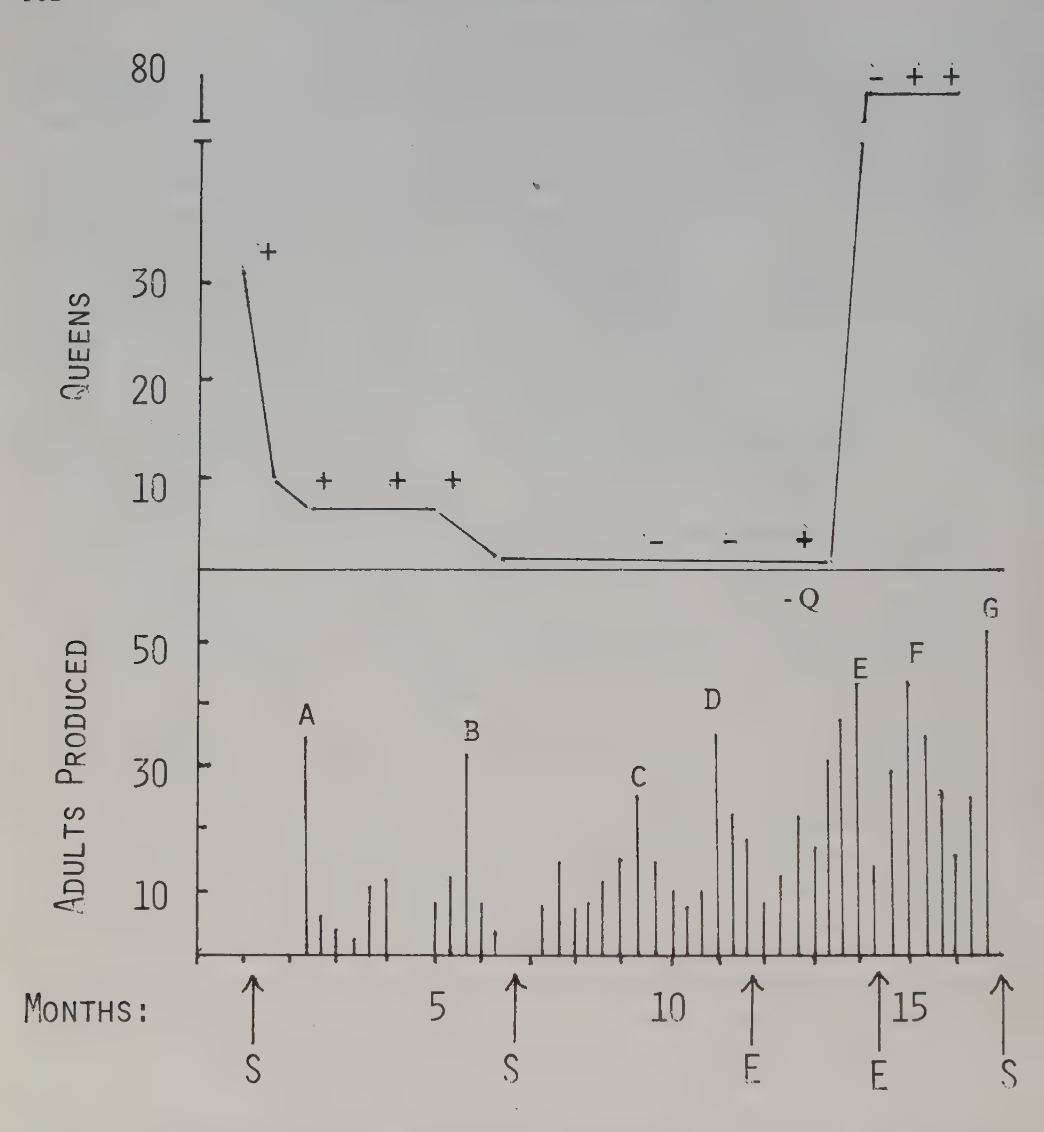


Fig. 1 – Timing of reproductive swarm emission in relation to adult emergence and queen agressiveness in a colony of *Metapolybia aztecoides*. Letters denote peaks (a-g) of production of adult females, swarm production (S), nest enlargement (E), and date of disappearance of single queen (-Q). Symbols + and - denote presence (+) and absence (-) of marked aggressiveness among queens.

Fig. 1 – Tiempo de emisión de reproductoras durante la enjambrazón en relación à la emergencia del adulto y la agresividad de la reina en una colonia de *Metapolybia aztecoides*. Las letras denotan picos (a-g) de producción de hembras adultas, producción de enjambre (s), agrandamiento del nido (E), y fecha de desaparición de la única reina (-Q). Símbolos + y - denotan la presencia (+) y ausencia (-) de agresividad marcada entre las reinas.

azteca Araujo and *Polybia occidentalis* (Olivier) in a markedly seasonal region of Costa Rica is associated with other seasonally synchronized events such as male production, aging of established queens, brood cannibalism, and aggression among young queens (Forsyth, 1978). The precise order in which these events occur, and the nature of and non-swarm-producing colonies, are not known. It is therefore of interest to examine the pattern of reproductive swarming observed in a colony of *Metapolybia aztecoides* whose history I followed closely for 18 months. In Cáli, Colombia (4° N latitude) *M. aztecoides* shows no obvious reproductive seasonality. Furthermore, no males were produced by this colony or its observed descendents during the 18 month observation period. However, 905 females were produced and marked. Colony fission (swarming with division of the colony into more than one group) occurred three times :

1. Nine days after colony foundation, 17 of the 35 founding queens left with an unknown number of workers. When pre-swarming activity (see below) was first observed, along with intensive fanning (cooling) activity, I placed a palm leaf on a roof above the nest to provide shade. When next observed, both swarming preparations and fanning had stopped among the remaining wasps, but a swarm had already departed. Thus colony fission apparently occurred in response to temporarily unfavorable conditions (overheating), with some wasps leaving and others staying.
2. Five months after colony foundation, half (3) of the remaining six foundress queens left with a large number of workers (110 had been produced), leading to a severe shortage of workers (only nine present prior to the next synchronous emergence). Swarming occurred 10-15 days after the peak of a large emergence, when the population of adults was the highest it had been since nest initiation.
3. Sixteen months after nest foundation, during the second of two major peaks of female production following a nest enlargement (see Fig. 1), two swarms, containing 200-250 and 92 individuals, abandoned the original nest and founded new nests less than 30 m. away.

Although the first swarm may have been an abortive absconding swarm (including only part of the colony because the nest was shaded), aggressiveness among queens was occurring and may have contributed to their readiness to fission. This nest was not obviously damaged until after the adults had absconded, when it quickly deteriorated as if chewed by a mouse. Just prior to swarming the envelope removed (routinely) to facilitate observation was not repaired by the wasps. It is possible that envelope removal, although not causing swarming during the previous 16 months, triggered swarming at this time of unprecedented population size and, also, brood immaturity following massive emergences (Fig. 1). It is also possible that the two swarms left

independently of each other, the first as a «reproductive» swarm and the second for some reason «absconding». (I was not present when the two swarms left). All three swarming events were preceded by brood cannibalism (eating of larvae) and marked aggressiveness among queens (bending threats, and vigorous «dancing» by workers – see West-Eberhard, 1978). Both instances of swarming in the mature colony followed massive emergences of adults (Fig. 1). The colony at those times was composed of unusually large numbers of adult females and unusually small numbers of large larvae and pupae. Pulsed, or cyclic, adult production is a common characteristic of swarm-founded colonies, especially in small-colony species. Adult emergence peaks occur because rapid comb construction and egg-laying by a swarm leads to synchronized emergence of adults followed by another round of (synchronous) egg laying. This cycle can persist for many months (see Fig. 1).

Although swarming in this colony followed peaks of adult production, not all peaks were followed by swarming. Analysis of the adult-production peaks *not* followed by swarming helps to further define the conditions leading to colony fission. Two peaks (d en a, Fig. 1) were followed by nest enlargement rather than swarming. In both these cases there was a notable absence of aggression among queens, following peak d because there was only a single well-developed (unchallenged) queen present, and following peak e because the large number of queens present were young, relatively undeveloped (having small ovaries), and not yet strongly competing (see West-Eberhard, 1981). The timing of events is also revealing : both swarming and nest enlargement occurred 10-15 days after emergence peaks, which corresponds to the time required for newly emerged females to show slight ovary development. If a dominant queen (s) is not present at that time, newly emerged *Metapolybia* females begin to lay eggs (see West-Eberhard, 1978).

These observations indicate that emergence peaks lead to colony fission indirectly, by causing a rise in the number of competing females (potential egg layers) on the nest. That is, reproductive swarming in *Metapolybia* is a product of reproductive competition involving newly emerged females rather than a simple consequence of crowding. When emergence peaks lead to nest enlargement rather than reproductive swarming, the young females (potential queens) play a disproportionately large role in enlarging the nest. Although 15-25 day-old females represented only 39 % of the adult population present following emergence peak d (Fig. 1) they made up 56 % of the females observed building the new comb. These females obtained pulp by tearing down the old envelope rather than foraging, and sometimes acted aggressive toward the monogynous queen when she visited the new comb. Building without foraging is a characteristical activity of young, somewhat ovary-developed, females and recently suppressed former queens (see West-Eberhard,

1981). Thus the activity of a newly-emerged female can be channelled either toward reproduction (and sometimes swarming) or toward enlarging the parental colony, depending upon the social circumstances in the colony soon after she emerges.

Some emergence peaks (a, c, and f) led to neither swarming nor nest enlargement. The newly emerged females simply became workers. In all these cases an established mature queen (c) or group of queens (a and f) was present, and the population of workers was low relative to the size of the colony. Following peak a there was can acute worker shortage due to the long delay in female production following nest founding, and all foraging was being performed by former queens. At peak c the crisis was less severe, but the adult population was low following a long period of low productivity after a swarm (Fig. 1). And at the time of peak f many would-be workers had become queens and were thus consuming foraged food rather than obtaining it. So emergence peaks in the presence of dominant queen(s) and worker scarcity lead to the production of workers without swarming or nest enlargement. This suggests that colony fission requires an abundant worker population in addition to reproductive competition among females. As already noted, swarming is associated with low populations of large larvae. Colony fission may prove predictable when peaks in the functional-worker/larva ratio coincide with peaks in reproductive competition among females.

Seasonal swarming occurs in many Polybiine wasps at intermediate latitudes (Table 2). So far little is known about the nesting cycles of these species. It is impossible to state whether extrinsic cues such as changes in daylength or humidity affect swarming, or whether synchrony is simply a consequence of marked seasonality in food availability and activity times leading to synchrony of brood production and (hence) swarming propensity. Seasonal swarming is not closely synchronized, but, at least in some regions, occurs during a 3-4 month period (e.g., see Machado, 1977).

PRE-SWARMING BEHAVIOR

Swarming is preceded by marked changes in the behavior of wasps at the nest. They are described below in approximate order of their occurence.

Pre-swarming pheromone release. The original stimulus to begin swarm preparations, at least in the case of absconding swarms, may be the release of a chemical alarm signal by disturbed individuals. This was suggested by a peculiar combination of circumstances while observing a large newly founded colony of *Synoeca surinama*. Directing very bright reflected sunlight on the comb (in order to film behavior) provoked synchronous strong alarm behavior.

Table II – Seasonal swarming in tropical social wasps (Polybiini)

Tabla II – Enjambrazón estacional en las avispas sociales tropicales (Polybiini)

Species	Months	Season	Place	Latitude	Source
Brachygastra lecheguana (Latr.)		early dry	Jalisco, Mexico	16° - 20° N	Buysson, 1905
Polybia occidentalis (Olivier)	Nov.-Jan. May-Aug.	mid rainy, early dry rainy	Guanacaste, Costa Rica	10°40' N	Forsyth, 1978
Metapolybia azteca	Oct.-Dec.-Jan. May-June	late rainy, early dry rainy	Guanacaste, Costa Rica	10°40'	Forsyth, 1978
Metapolybia pediculata Sauss.	Aug.-Sept.		Panama	9°10'N	Rau, 1933
Protopolybia acutiscutis (Cameron)	May-June	late dry	Panama	9°10'N	Naumann, 1970
Epipona tatua (Cuv.)	late Dec. mid June	early dry	Cayenne, Fr. Guiana	5°N	Lacordaire, 1838
Polybia ruficeps Schrottky	Sept.-Oct.	dry	Mato Grosso, Brazil	12°50'S	Richards, 1978
Polybia occidentalis (Olivier)	May-June Sept.-Oct.	dry	Rio Claro, Brazil	22°25'S	Machado, 1977
Parachartergus apicalis (F.)	April-May	winter	Alto Parana, Paraguay	24° - 25° S	Bertoni, 1912
Polybia occidentalis		late summer	Mercedes, Uruguay	33°S	Brethes, 1903
Polybia scutellaris (White)	Oct. Nov.-Dec.	early summer late dry	Argentina Rio Claro, Brazil	34°55'S 22°25'S	Bruch, 1936 Rodrigues, 1968

Several individuals immediately began performing buzzing runs and loop flights (see below) which were taken up by others within a short time, and all building activity ceased. My face was close to the nest when this occurred (protected by a head net) and I soon felt a stinging irritation in both eyes which became watery and swollen. This sensation (an allergic reaction) was relieved when I moved away from the nest. Although close inspection of alarmed individuals revealed no special postures or extruded stings suggesting pheromone release, I believe that a diffusable alarm substance was being produced which I (being hypersensitive to wasp tissues and venoms) was able to detect. Naumann (1970) also believes that a pre-swarming alarm substance may be released by buzzing runners in *Protopolybia* and has noticed that they sometimes hold the abdomen high «extended and noticeably recurved or decurved as if releasing a substance» (p. 122).

Regrouping. If the nest has been destroyed or attacked (e.g., by army ants) the resident adults quickly abandon the nest and then form a cluster close to the nest site. I have observed this in an absconding colony of *Polybia raui* whose nest was severely damaged when rain caused a landslide in the roadbank where it was attached to a root ; and it is common when nests are destroyed by man. Chadab (1979) observed regrouping following 19 army ant raids on a variety of neotropical polybiines, and found that regrouping was completed an average of 72 minutes after nest abondonment (range 21-190 minutes). Jeanne (1981) saw profuse abdominal «dragging» (scent marking) of the regrouping site in *Polybia sericea*. Dragging ceased once the temporary cluster was formed, then began again during trail marking (see below).

Buzzing runs (called «breaking behavior» by Naumann, 1975). Excited running by a few to many individuals is the most characteristic and widespread pre-swarming behavior noted by observers (e.g. Bruch, 1936 ; Naumann, 1970 ; Jeanne, 1975a ; Forsyth, 1978). It is this behavior on the nest that is the first definite cue that swarming is likely to occur. When absconding swarms are provoked by a sudden event (such as the shining of a bright light on the nest) buzzing runs are an immediate reaction which continues with increasing intensity until the wasps leave. They were first mentioned by Bruch (1936), who saw wasps running and turning («volteando») in a colony of *Polybia scutellaris* before it swarmed. Some wasps (probably scouts) returning to the nest run erratically about, occasionally engaging in brief mouthpart contact with encountered nestmates, then suddenly take flight. Sometimes the wings are raised, and at high intensity the wings are buzzed, and the running wasp seems to tumble about crazily bumping into other. In *Synoeca surinama* workers performing buzzing runs showed typical «offering» behavior (mandibles raised, antennae motionless) accompagnied by rapid lateral shaking and followed by mounthpart contact with encountered nestmates.

At low intensity this behavior seems to cause no reaction in the wasps on the nest, but at high intensity it sometimes causes clusters to break up and activity to rise, with an increasing number of wasps performing similar runs.

Buzzing runs are similar in apperance and function to several other kinds of behavior in social wasps. The «parasite alarm» of *Polistes* (West-Eberhard, 1969) and many other genera (observed by me in *Polybia emaciata, Polybia diguetana, Metapolybia aztecoides,* and *Synoeca surinama* ; and by Naumann, 1970, in *Protopolybia acutiscutis*) resembles pre-swarming buzzing runs in that the performer moves errativally around the comb jerking near nestmates, and often flipping the wings, sometimes causing others to do the same. The parasite alarm movements are more rhythmic than the buzzing runs, and can almost always be associated with the presence of some brood parasite, such as an ichneumon wasp or phorid fly. However, the behaviors are so similar that they are sometimes confused until the context of the behavior can be ascertained. If foraging continues and there is little change in intensity or numbers performing buzzing runs they probably represent anti-parasitoid behavior. As noted by Naumann (1970, p. 122) buzzing runs sometimes occur in response to severe disturbance (such as seizing an individual with forceps) without leading to swarming. It is unknown how many individuals (or which ones) must be stimulated to provoke swarming. Buzzing runs are remarkably similar to the «Schwirrlaufen» performed by swarming honeybee scouts (Lindauer, 1955 ; Seeley et al., 1979), which similarly rise in frequency prior to swarm liftoff (Seeley et al., 1979). All of these behaviors incorporate either fast runs, wing buzzing, bumping nestmates, rapid shaking, or brief mouthpart contact or some combination of these elements. And all seem to stimulate movement and/or flight in nestmates.

Because this behavior is at first performed by a few individuals who repeatedly leave the nest and return loadless, it seems likely that these are the individuals («scouts») active in choosing a new nest site and/or marking the trail followed by the swarm. The suspicion that this is the case is reinforced by the observation that in *Metapolybia* a disproportionate number of females performing buzzing runs and repeated trips away from the nest are old foragers – the females most familiar with the surrounding area and most prone to searching activities away from the nest. During the hour just prior to swarming in a colony of *M. aztecoides* only 15 (16.7 %) of the 92 females present performed buzzing runs. Nearly one third of these females were known foragers more than two months old, even though this age class made up only 10 % of the population present. The remainder were younger females of unknown foraging history. None was a queen. Similarly, during two hours of observation on the first day of swarming preparations following predation on a nest of *Synoeca surinama*, only eight (7,6 %) of the 105 females present

performed buzzing runs. All were old (72 days or more) members of the swarm which had founded the nest nine weeks before. None of the 77 younger offspring of that colony (females 1-21 days old) performed buzzing runs. Forsyth (1978) likewise found that marked wasps performing buzzing runs prior to swarming in *Polybia occidentalis* were known foragers. He also observed that these individuals were active in initiation and construction of the new nest, althought they sometimes switched to other (non-foraging) roles once the nest was established.

Unusual readiness to fly when disturbed. Once buzzing runs have runs have started, events, (such as envelope removal or marking of individuals with paint) usually causing no reaction, lead instead to flying off the nest (observed in *Synoeca surinama* and *Metapolybia aztecoides*). Increased alertness and readiness to fly may be a consequence of the buzzing runs, which (as just described) resemble other kinds of alarm behavior perhaps leading to readiness to attack or chase an intruder.

Loop flights. During the pre-swarming period many individuals take flight briefly, then return to the nest where they perform buzzing runs or simply land. Forsyth (1978, p. 139) has described these short «loop flights» in *P. occidentalis* as follow : «relatively slow flights of circular motion with the wasp usually facing the nest and looping in a radius of 0.5 to 2 meters». As the wasp hovers near the nest during a loop flight nestmates in that region often take flight and begin performing loop flights themselves.

Hovering near the nest has been observed to stimulate flight in several contexts other than swarming. For example, in *Polybia diguetana* R. du Buysson females performed loop flights near the nest entrance for more than an hour while a phorid fly (a common brood parasitoid) was on the nest. Their behavior, which also included buzzing runs, was distinguishable from pre-swarming behavior only because normal foraging and building continued, and individuals returning to the nest from long flights never participated (as would swarm «scouts»). Individuals on the nest sometimes walked forward or flex when approached by a hovering nestmate. Machado (pers. comm.) reports that loop flights occur in *Polybia paulista* when flying aggregations of «lambe-olho» flies (Diptera, Chloropidae) occur near the nest.

In *Metapolybia aztecoides* loop flights occur without relation to either distance and hover facing the nest, causing others near them to take flight and perform similar flights until all individuals present (including the usually passive queens) have left the nest. Some fly about the area as if searching ; and although they appear aggressive and alarmed they do not sting even objects within a few centimeters of the nest. Eventually all return, and normal activity is resumed. False swarming creates a frightening airborne mass of wasps near the nest, and migh function to intimidate some predators. However,

it is not clearly associated with any threat to the nest, and I believe it may sometimes be initiated by the slow hovering approach of heavily laden foragers. (A small false swarm occured in *Parachartergus apicalis* when a strong wind forced approaching wasps to hover before the entrance, causing others to take flight as in the false swarming of *Metapolybia*). Whatever the adaptive significance (if any) of false swarming, just as in true swarming, hovering loop flights seem to stimulate leaving the nest even by normally non-flying individuals (queens, and newly emerged females). Loop flights observed in *Polybia raui* increased dramatically just prior to liftoff of the swarm (Fig. 2). Forsyth (1978), p. 140) believes that leaving the nest is «relatively directional» and «appears to be guided by the looping activity of scouts». I have noticed marked changes in the shapes and positions of clustered wasps prior to liftoff in *P. raui* and *P. liliacea*, which appear to be directional in nature (e.g., rotation from one side of the nest to another ; and increased compactness of a regrouped cluster accompanied by a bulging in the side toward the new nest site). The possibility that loop flights function in the initial orientation of the swarm merits further investigation.

Clustering on the surface of the nest. Naumann (1970) photographed this phenomenon in *Protopolybia acutiscutis* (Cameron) (Naumann's specimens were recently identified by O.W. Richards according to Jeanne, pers. comm. ; called *P. pumila* by Naumann, 1970) and I have observed it in an absconding colony of *Polybia liliacea* attacked by termites. In the latter case the clusters persisted throughout the day prior to swarming, sometimes changing position. At noon the day before swarming occurred (at 7:05 a.m.) the wasps were concentrated on the windward side of the large nest while dispersed on the opposite side, but 1.5 hours later the cluster had shifted to the opposite side although the wind direction had not changed. I attempted to see if the location of the rotating cluster could be used to predict the direction of the swarming, but could not discern the path of the trail at the time the swarm left. The nest was about 10 m high in a tree and the thousands of circling wasps were soon lost to my view (see «liftoff, below).

Building arrest. Even if the wasps have not left the nest, one sign that it will soon be abandoned is the marked reduction or cessation of pulp foraging and additions to envelope and comb. I have noted this in *Metapolybia azracoides, Polybia liliacea, Polybia sericea,* and *Synoeca surinama.*

Brood cannibalism and aggressive begging. Eating of large larvae and pupae (but not eggs and small larvae) by workers occurred prior to both absconding and reproductive swarms in *Metapolybia aztecoides*, prior to absconding in *Synoeca surinama* (reproductive swarms were not observed in that species), and prior to swarming in *Protopolybia acutiscutis* (Naumann, 1970). Recently abandoned nests of *Polybia sericea* and *P. liliacea* contained

eggs and small larvae, but no large larvae or pupae. In a pre-swarming colony of *S. surinama* all brood abortion was performed by old workers ; young (1-21 days old) females did not participate, and showed no interest in eating larvae seized by the others (there were no females of intermediate age present). Although building activity stopped during pre-swarming activities as already described, foraging for food continues. In *Polybia sericea* I once observed strikingly aggressive solicitation by nest wasps of returning foragers during the four days prior to absconding. Returnees were literally mobbed and violently attacked by up to ten nestmates at a time. Wasps waiting on the envelope sometimes attacked slowly approaching foragers in the air and once desperately solicited from each other in fruitless frenzy when unable to locate a returning forager that had landed on a nearby leaf. Two attacked workers that were captured and dissected proved to be old (dark apodemes – see West-Eberhard, 1975) mated females with discolored spermathecae and signs of former ovary development. Two dissected attackers were both unmated young (light apodemes) females with undeveloped ovaries. The dissected individuals provide a possible explanation for the aggressiveness of solicitation observed : the attacked workers were «reserve» foragers – former queens that probably became workers during a shortage of workers as is known to occur in other species (see West-Eberhard, 1981). And the solicitors were very young females, perhaps too young (less than 10-15 days) to have begun foraging. Thus this colony may only recently have produced offspring females after absconding from a previous site leading to an acute shortage of foragers and inability to quickly enough bring food to meet the pre-swarming demands of non-foraging adults. This demand did seem associated with preparations to swarm : the same colony observed six days later at the new nest no longer showed aggressive solicitation of returnees although a large cluster of idle wasps was present. Aggressive begging was not observed in other pre-swarm colonies, perhaps because enough workers were present to supply the apparently increased demands of nestmates prior to swarming.

Trail marking. The «dragging» behavior, or rubbing of the ventral surface of the gaster on substrates at intervals between new and old nest sites, has been well-described by Naumann (1975) and Jeanne (1975a). So far it has been seen in six of the 23 genera of «swarming» polybiine wasps, namely, in *Angiopolybia* (Naumann, 1975 ; Chadab & Rettenmeyer, 1979), *Leipomeles* (Naumann, 1975), *Stelopolybia* (Naumann, 1975 ; Jeanne, 1975a ; pers. obs. of *S. areata* and *S. hamiltoni*), *Synoeca* (pers. obs.), *Parachartergus* (pers. obs.), and in several species of *Polybia* (Naumann, 1975 ; Jeanne, 1981 ; Forsyth, 1978 ; pers. obs.). It presumably occurs in all swarming genera ; at least none have been known to coordinate swarm movement by any other means. The Richard's organ associated with production of the trail pheromone

is present in 16 of the 18 genera examined (Richards, 1978 ; see also Landolt and Akre, 1979 ; Jeanne and Post, in press). Of the two species (*Angiopolybia pallens* and *Leipomeles dorsata*) in which glands were lacking, one (*L. dorsata*) is known to perform abdomen dragging along the swarm trail (Naumann, 1975).

Jeanne (1981) reports that movies of dragging behavior in *Polybia sericea* show that the fifth gastral sternite is applied to the rubbed surface during dragging. He was able to induce swarming wasps to follow an artificial trail made by rubbing the glandular («Richards'organ») region of that segment on pieces of filter paper that were in turn placed along a row of stakes in the field. He (but not his assistant) can smell the Richards'gland secretion on leaves, and finds that it has a distinctive leatherlike odor.

Scent trails are apparently not used in very short (less than 20 m.) absconding swarms (Forsyth, 1978 ; Chadab, 1979 ; Chadab & Rettenmeyer, 1979 ; pers. obs. of *P. raui*), although the new nest site itself may be heavily marked. This is not surprising since wasps marking and following scent trails regularly fly several meters between marks. In Jeanne's experiment scent marks were placed four meters apart. Trails are sometimes diffuse in that different scouts mark different routes to the same site. (pers. obs. of *S. surinama*). Jeanne (1975a) has observed wasps dragging as far apart as 10 m. along a line perpendicular to the direction of swarm movement. Although previous reports do not state whether dragging occurred during incoming or outgoing trips to (or from) the old nest, or both, my observations of trail marking in *S. surinama* revealed that early in trail marking dragging occurred only on incoming trips. During that period outgoing wasps only followed trails, pressing the tips of their antennae against landing surfaces as described by Naumann (1970), Jeanne (1975), and Forsyth (1978). However, within an hour of liftoff I noticed that wasps were marking on outgoing trips as well.

Jeanne (1981) reports that in colonies that have not recently swarmed females have thick deposits of brownish viscous secretion over the Richards' gland. In recently migrated colonies, on the other hand, this substance is depleted, especially in older individuals. Richards (1978) states that in some collected colonies queens can be distinguished from workers by the greater accumulation of secretion over their Richards'gland, which he therefore believed might be a «queen substance» involved in maintenance of reproductive dominance within the colony (see below). Whatever its functions, the accumulation may simply be due to the often greater age of queens, and the fact that they do not participate in swarm trail marking (allowing for a greater accumulation of secretion) (see Jeanne, 1981).

Temporary aggregations along the swarming route prior to liftoff. Forsyth (1978) observed that *Polybia occidentalis* scouts form small aggregations

near the nest along the trail being marked. The positions of these aggregations eventually become fixed, and the loop flights (see below) are made between the old nest and the nearest aggregation, giving a strong directionality to the flights and causing the aggregation to grow as the short flights increase in frequency (see below).

Nest initiation prior to swarm arrival. Some species (*Polybia velutina* – Chadab, 1979 ; *Polybia sericea* – Jeanne, 1981 ; *Apoica pallens* – Naumann, 1975) at least sometimes begin construction of the new nest before the swarm arrives. In other cases observers at a new nest site have noted swarm arrival without previous building (e.g., in a *Synoeca* species, probably *septentrionalis* Richards, observed by R. Matthews and C. Starr in Costa Rica and in *Polybia scutellaris* – Bruch, 1936). In *Synoeca surinama* I saw some individuals carrying pulp along a swarm trail during the time that the main body of the swarm was passing my observation place, suggesting that building had already begun. Unfortunately I was unable to pursue the wasps across an anaconda-infested swamp to the new site.

The pre-liftoff preparations described above occupy from five hours to four days in the case of absconding swarms (Chadab, 1979). The average for 20 swarms representing a wide variety of genera raided by army ants was 20.7 hours (Chadab, 1979). As pointed out by Chadab (1979), one factor affecting the time required for absconding preparations is probably the amount of time required to find a suitable new nest site. The longest preliftoff time she observed (four days) was for a colony of *Polybia rejecta*, a species usually nesting in trees containing large colonies of ants (*Azteca*). The long preparation time may have reflected the difficulty of finding such a site.

SWARM MOVEMENT

Liftoff. Following the sudden rise in frequency of loop flights (Fig. 2) the wasps begin to leave the vicinity of the nest rather than return to it. It is difficult to pinpoint the exact moment at which this change in behavior occurs, because the loop flights are accompanied by longer flights (of varying length) away from the nest, and the loop flights themselves may lengthen with time (I was unable to document this possibility). The observer is only sure that liftoff has occurred when it is over : wasps seem to fill the air, and the number on the nest or in the regrouped cluster declines. Then, within a few minutes, they are gone, leaving only a few stragglers on the nest or broadly circling nearby.

Trail following. In all seven species whose swarm movement I have observed (Table I) wasps seem to follow the trail to the new site as individuals.

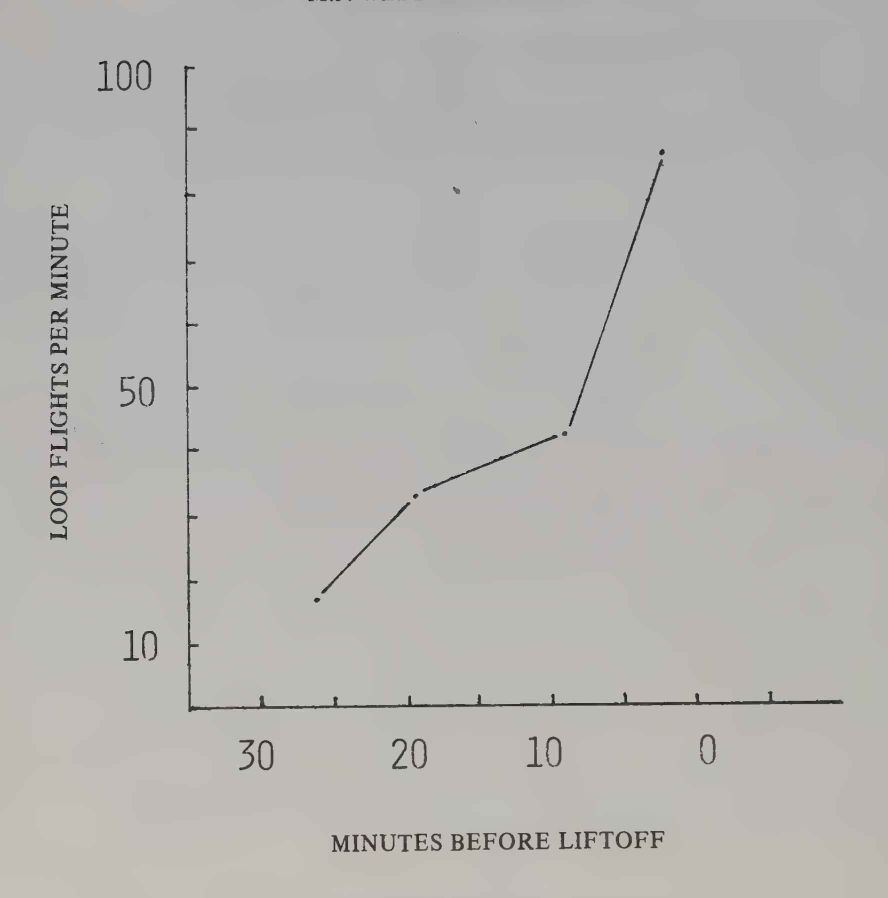


Fig. 2 – Frequency of loop flights prior to swarm liftoff in *Polybia raui*

Fig. 2 – Frecuencia de vuelos en forma de U anteriores a la elevación del enjambre en *Polybia raui*

That is, each female seeks landmarks one after another rather than following a straght line to the end ; and each wasp seems to fly and search for marked sites on her own, rather than in a group or in response to the movements of others. Although clusters may form along the route (see below) wasps do not form moving clusters in the air as do honeybees and the swarms of wasps are less compact. While a swarm of 10,000 honeybees occupies a «circular» volume about 10 m. in diameter and 3 m. high (Seeley et al., 1978) large diffuse swarms of wasps (e.g., *Stelopolybia* species) are commonly spread over an area up to 100 m long and 20-50 m wide. They sometimes take more than

more than 30 minutes to pass a given point, with stragglers visible for 30 additional minutes (pers. obs.).

The behavior of a trail-following wasp resembles that of a forager in that she visits and inspects vegetation and other objects somewhat erratically as she flies along. However, the following observed features of trail-marking and trail-following behavior probably help to facilitate directional movement :

1. Use of prominent landmarks. Scouts mark (and followers inspect) mainly conspicuous or protruding surfaces, e.g., the tops of shrubs, isolated plants in clearings, the apical leaf of a branch, or the top of a fencepost. An observer (and presumably a wasp) can predict which objects along a trail are likely to be used, and this consistency in choice must increase the efficiency of the trail.

2. Conservation of direction and altitude. Trail followers leaving a marked site tend to continue in the flight direction with which they approached it. If the next most prominent objects in an approximately straight line prove to be unmarked, the area soon fills with temporarily disoriented, searching wasps. As a result there is much disorientation and «piling up» of wasps at turns, whether they are to the side or vertical (e.g., up into the canopy of a tree, or down into a ravine). Turning disorientation is particularly obvious in very large swarms. A spectacularly large swarm of *Stelopolybia areata*, containing uncountable thousands of wasps (Jeanne, 1975b, estimated the adult population of a colony of this species at 21,800) occupied an area only 2-3 m wide when moving along a straight path. However, when forced to turn to move past a house, searching wasps were spread over an area 50 m wide. Disoriented individuals must sometimes be permanently lost. These two behaviors – use of prominant landmarks, and conservation of direction – mean that swarming wasps readily follow clear topographical features such as fencelines, trails, roadcuts, and the edges of clearings (noted by Jeanne, 1975a in *Stelopolybia areata* ; pers. obs. of *Synoeca surinama*).

3. Close spacing of marked sites at turns. The abdomen rubbing activities of scent-marking wasps are particularly frequent at turning points. This must serve to reorient searchers and «anchor» them to the point where the search for the next mark must begin, thus helping to reduce turning disorientation.

Clumped swarms. Some species (*Polybia ignobilis, P. raui*, and *Parachartergus apicalis*) at least sometimes form temporary, compact clusters at intervals along the the swarm route. Clusters are spaced about as far apart as the scent-marked sites of other species, and occupy similar kinds of sites. As the swarm progresses the forward-most clusters grow, while those behind dissolve. A clumped swarm of *P. raui* was remarkable for the absence of scent marking, at least during the two hours it was observed. Although many wasps searched vegetation between four clusters, none rubbed its abdomen on

objects between cluster sites. When I placed the plant abandoned by one cluster in the path of wasps moving between two others they paid no special attention to it. And when a second site was abandoned, passing wasps were not attracted to leaves which had been covered with swarm females only minutes before. Thus, if the leaves at these cluster sites are initially chemically marked, they are no longer attractive when the wasps leave. Similarly, scent marking was very infrequent (1-2 times/observation hour) in a clumped swarm of *Parachartergus apicalis* even on a «difficult» route between two clusters (more than 50 meters, circumnavigating a tall building). However, the moving wasps behaved as if following a scent trail, most taking the same route, searching vegetation, and showing disorientation at turns. By contrast, a small diffuse swarm of *P. apicalis** scent-marked frequently. When successive clusters are closely spaced and within sight of each other, as the were in the *Polybia raui* swarm, wasps may not employ scent marks. Cluster sites are conscicuous (to me) because constant loop flights (26/minute in a 50-wasp cluster of *Parachartergus apicalis*) surround them with a cloud of moving wasps. This may facilitate visual orientation. There was no obvious scenting behavior (abdomen dragging or raising) at the site of a newly initiated, growing cluster of *Parachartergus apicalis*. Clumped swarms appear to progress much more slowly than do diffuse swarms. The approximate center (densest portion) of the large swarm of *Stelopolybia areata* moved an estimated average 17.5 meters per minute (1.05 km per hour), even when the 200 m timed path included two difficult obstacles (a deep ravine, and a house). An observer must keep moving quickly to follow such a swarm, whereas the clumped swarms I have observed, while not precisely timed, require several minutes or even hours to advance by one cluster (with 20 m the maximum distance I have recorded between cluster sites). Dissolving clusters, while a relatively slow mode of movement, may have the advantage of reducing losses due to disorientation.

Small short-lived cluster sometimes occur in diffuse swarms, and along the route between large cluster, in *P. apicalis*. Searching females seem attracted to leaves where others are sitting. Such «piling up» during diffuse swarm movement may have been a precursor of clumped swarming. Future research should reveal whether these two swarming patterns – clumped, and diffuse – are strictly species specific or situation dependent, and whether or not pheromones are employed differently in the two modes.

* Two somewhat divergent populations (species ?) were identified by O.W. Richards as *P. apicalis* (see Richards, 1978) : one at 1350 m (San Antonio de Escazu, hills S.W. of San Jose) with diffuse swarms and a truncated conical nest entrance ; and another at 1200 m (San Pedro de Montes de Oca, east of San Jose), with clumped swarms and a tubular nest entrance. Specimens are deposited in the British Museum (Entomology).

Overnight resting clusters. Diffuse swarms sometimes rest in compact clusters at night en route to a new nest site. Rau (1933) observed that a cluster of *Polybia emaciata* Lucas remained for two days on a wire not resembling a nest site on Orchid Island (Gatun Lake, Panama). Jeanne (1975a) followed the movements of a diffuse swarm of *Stelopolybia areata* in Mexico, and found that it moved 70-100 meters per day, resting as a cluster on trees at night.

Length of migrations. As pointed out by Forsyth (1978) it would be of great interest in understanding the population structures of social wasps to know the migration distances of reproductive and absconding swarms. Unfortunately, such information is very difficult to obtain. I have repeatedly tried in vain to follow swarms of *Metapolybia aztecoides*, but have been frustated by their small size and the apparent diffuseness of their swarms. Even after two full days following the pre-swarming behavior of *Polybia liliacea*, a relatively large wasp, I was unable to follow the swarm, which diffused in a spectacular liftoff up into the canopy of a large tree and disappeared from view. It is sometimes possible to locate new nests of marked colonies after swarming. Two new nests of *Metapolybia aztecoides*, representing the entire population of an abandoned nest, were found within 20 m of the old site. An a marked colony of *Polybia sericea* relocated 250 m from its abandoned nest. Much longer migrations probably occur. The longest documented one I know of is 319 m in four days, by an absconding swarm of *Stelopolybia areata* (Jeanne, 1975a). The total migration may have been longer, as nest building had not begun when the observations ceased. It is quite common for absconding swarms to nest within a few meters of an abandoned site. Chadab (1979) lists the relocation distances for 17 colonies of seven polybiine species raided by army ants. All began construction only 0.3-2.0 m from the abandoned nest. Chadab notes that these values are likely to be somewhat unrepresentative because of the difficulty of finding more distant new sites. As suggested by Forsyth (1978) the upper limit for migration distance may be the foraging range of the foragers who act as scouts.

Behavior at the new site. I have only once observed the arrival of a swarm at a new nest site. In that case, a swarm of *Stelopolybia hamiltoni* moving into an enclosure (a cardboard box) many wasps were abdomen dragging the enclosure entrance as the swarm arrived, and many stood or walked nearby with abdomens raised and wings buzzing. These wasps were already aggressively defending the new site, in contrast to their passivity toward observers while en route.

The composition of swarms. Absconding swarms must often contain all of the adult female members of a colony. When this is the case, their age and caste composition would simply depend on that present when absconding

happens to occur. However, Forsyth (1978) reports that absconding by *Metapolybia azteca* following army ant raids sometimes leads to colony fission. The causes and consequences for colony composition of such splitting are unknown. Forsyth (1978) took advantage of the seasonal swarming habit of *Metapolybia azteca* and *Polybia occidentalis* in Costa Rica to estimate the composition of reproductive swarms. Since he observed predation destruction of nests to be low during swarming seasons, swarms collected at those times were presumed likely to be reproductive rather than absconding swarms. Ten dissected seasonal swarms of *M. azteca* contained 1-36 queens (mean = 11), and 16-174 workers (mean = 66.8). And ten dissected swarms of *Polybia occidentalis* contained 2-21 queens each (mean = 7.8), and from 69-350 workers (mean = 223.6). Males have never been observed to actually move along with a swarm, but there are several reports of males at very new nest sites. Ducke (1905) observed males in a nestless swarm of *Apoica pallida* ; and Richards (1978) found males with females from a very new nest of *Apoica flavissima* in the collection of the Museu Paulista (Sao Paulo, Brazil). He also cites Rodrigues (1969) as reporting males in a 45-day-old colony of *Polybia occidentalis* var. *scutellaris*, and speculates that they may have been present in the founding swarm. However, Machado (1977) has since found that the egg-to-adult developmental time in that species can be as short as 35 days, so it is possible that the males were produced there. I have observed males with a swarm of *Leipomeles dorsata* during the first day of nest construction, and at a pre-emergence nest of *Parachartergus colobop tera*, where their attempts to enter the nest resembled those of parasitic wasps and flies. Like parasitoids, these male were vigorously chased by attendant workers. In none of these cases is it known whether the males followed the swarm trail or arrived at the new site later.

THE EVOLUTION OF SWARMING IN WASPS

Explaining the origin of a complex coordinated activity like swarming can be approached via the comparative study of related forms. Fortunately, in the case of the social wasps there are several non-swarming genera (*Belonogaster, Ropalidia, Polistes, Mischocyttarus*, and *Parapolybia*) belonging to the same subfamily (Polistinae) as the swarming species. Observations of these genera offer a few clues regardind the possible origins of coordinated long-distance migration.

Functions of the sternal glands in non-swarming social wasps

The «Richards'gland» of the fifth abdominal sternite, source of the swarm trail pheromone, is the one morphological feature with which we can begin searching for homologies in non-swarming species. Examining the functions of the sternal gland secretions in these groups may provide clues as to the origin of trail marking. The Richards' gland is present in examined species of *Polistes* and *Mischocyttarus* (Hermann and Dirks, 1974 ; Landolt and Akre, 1979 ; Post and Jeanne, 1980 ; Richards, 1978 ; Turillazzi, 1979) while being absent or not easily distinguished in *Belonogaster* and *Ropalidia* (*Parapolybia* has apparently not been examined) (Richards, 1978). The function of the Richards'gland secretion in non-swarming species is unknown : it has never been isolated for identification or subjected to behavior experiments. However, in many non-swarming species the abdomen is frequently rubbed or wagged on the surface of the nest. One type of abdomen rubbing – stroking of the nest top and pedical by the terminal abdominal sternite – in *Mischocyttarus, Polistes,* and *Belonogaster* species, has been shown to involve application of an ant repellent substance produced by the van der Vecht's gland of the seventh abdominal sternite (Jeanne, 1972. See recent summaries in Jeanne, 1975c and Post and Jeanne, 1981). Some authors (e.g., Hermann and Dirks, 1974 ; Turilazzi, 1979 ; cf. Post and Jeanne, 1980) assume that the Richards'gland has the same function. However, two kinds of observations suggest another or additional function of abdomen rubbing and the associated glands : some species that rub the pedical with the abdomen are nonetheless readily invaved by ants (e.g., *Ropalidia cincta* – Darchen, 1976), and *R. cyathiformis* – Gadagkar and West-Eberhard, in prep) ; and abdomen rubbing occurs in situations that suggest an association with social dominance and territoriality rather than nest defense. For example, queens (but not workers) of *Ropalidia marginata* and *Polistes canadensis* stroke the nest surface with their abdomens as they move across the region containing eggs (at the bottom of the nest rather than near the pedical) ; and workers of an unidentified *Polistes* species abdomen stroked the bodies of newly emerged females (Raveret and Richter, 1980), a class of individuals often special objects of aggression and domination in social wasps (see West-Eberhard, 1978 ; Gadagkar and West-Eberhard, in prep.). Both abdomen wagging (a variable intensity side-to-side movement of the abdomen against the surface of the nest, often producing a soft or sharp rattling sound on the comb) and abdomen stroking (a sinuous rubbing of the abdomen on the nest surface by a walking female) are associated with dominance and/or territoriality in *Polistes, Ropalidia,* and *Vespula* species (Maher, 1976 ; Gamboa and Dew 1981 ; Jeanne, 1977 ; Greene et al., 1978, pers. obs. of *Ropalidia ciathiformis,*

Polistes canadensis canadensis, and *P. major* in which it is performed most frequently by egg-layers).

Behavior observations thus suggest that sternal gland secretions of non-swarming species may function widely as dominance signals and territorial scents, in addition to sometimes being anti-predator secretions. It is therefore reasonable to hypothesize that the Richards'gland secretion functioned in one or all of these contexts in the ancestors of swarming species, then came to be used to mark the route to new nest sites (see below). Since the abdomen stroking (and possible sternal gland pheromone production) of non-swarming species is so often dominance related, it is of interest to note that queens of some swarming species are distinguished from workers in having a conspicuous accumulation of waxy secretion over the Richards'gland (Richards, 1970, 1978 ; pers. obs. of *Stelopolybia areata* and *S. hamiltoni*). It would be of interest to investigate the possibility that the gaster-bending behavior of queens in a variety of Polybiine genera (see West-Eberhard, 1977, p. 226 ; Naumann, 1970) serves to expose the Richards'gland. (As pointed out by Spradbery, 1973, the greater distension of a developed queen's oocytefilled gaster separates the sternites, exposing the sternal glands even when the queen is at rest). If the Richards'gland secretion does serve a double function, as a queen-recognition pheromone within the nest, and a trail-marking pheromone during swarming, it would provide a striking parallel with the double function of the honeybee «queen substance» that, within the nest, contributes to reproductive suppression of nestmates, and outside the nest causes clustering by swarming bees (see Michener, 1974, pp. 135, 361).

Swarm-like behavior in non-swarming species

Polistinae. Quasi-swarming – movements of nestmates from an old to a new nest site with some at least rudimentary communication or coordination en route – has been observed in a few non-swarming species. A marked *P. erythrocephalus* queen and ten nestmates whose nest (nest V6, see West-Eberhard, 1969, p. 63) was destroyed by ants first regrouped about one meter from their original nest site. The queen remained there for a day, with from 2-8 nestmates clustered with her or nearby. She sometimes moved to join others, rather than the reverse – the queen was not necessarily the nucleus of the group. However, these wasps did not join the more than 40 others associated with five newly founded nests in the vicinity ; nor did foreign wasps join them. Thus nestmates apparently recognized each other. Four days later the entire group of 11 wasps permanently occuped a nest founded two days earlier by another female about two meters from their original nest site. Similar loosely coordinated short migrations were noted by Litte (1976) in

Florida populations of *Mischocyttarus mexicanus*. Marked wasps from three abandoned nests formed shifting aggregations of up to 34 nestmates on leaves within five meters of abandoned nets. Some persisted for 38 days following nest abandonment. Two of these groups initiated nests one and five meters from their respective natal nest sites.

A striking example of quasi-swarming behavior in non-swarming wasps was observed by Litte in Colombian *Mischocyttarus labiatus* (Litte, in press). The population studied was heavily parasitized by phorid flies, that provoked frequent nest abandonment and renesting. Queens, leaving or returning to their new nests, dragged their abdomens over leaves and stems in the area between the old and the new sites. Other wasps landed on and antennated these rubbed surfaces. Queens also «abdomen dragged» near nests when nestmates disappeared or were experimentally removed. And Litte twice saw subordinate females from abandoned nests «abdomen drag» between new nests started by themselves and new nests started by dominant queens, in an apparent attempt to recruit nestmates. This is the first report of apparent scent-marking, resembling that of swarm scouts, in a non-swarming polybiine wasp. It is of interest that it occurs in a species having an unusually high rate of parasitization and renesting (Litte, in press), and that it apparently involves either or both the sternal glands present in others species of this genus (Richards, 1978 ; Landolt and Akre, 1979) but not previously known to be used in the context of nest site location or recruitment.

Vespinae. Another phenomenon very much like swarming is the mid-season «translocation» of nests by *Vespa crabro flavofasciata* Cameron and *V. simillima* Smith in southern Japan (Edwards, 1980, after Matsuura, pers. comm.). When early nest sites become too small for the growing nest, 30-100 workers («scouts») search the surrounding area for new sites, and form aggretations away from the nest. At first they settle in several sites, eventually congregating in only one. Meanwhile, as in the case of pre-swarming behavior in tropical polybiines, enlargement of the original nest ceases, and the queen stops laying eggs. When the queen flies to the new site nest construction begins. Some workers continue to feed larvae and newly emerged adults at the old nest for about a month, but eventually it is abandoned. Since new nests can be as far as 180 m from the old nest it would be of great interest to know how the new site is located. As many as 60 % of *Vespa simillina* colonies translocate their nests in this manner.

Possible stages in the evolution of swarming in wasps

Observations of non-swarming and primitively-swarming wasps suggest the following series of hypothetical steps in the evolution of swarming in this group :

1. Application of a repellent scent or territorial marker to the nest surface, as commonly observed in non-swarming species (aboves).
2. Use of sternal gland scents as assembly pheromones. Such scents applied to temporary resting places or newly founded nests might serve to attract, or keep together nestmates that have left the parental nest, like the assembly pheromone postulated for *Vespa* and *Polistes* (called «building initiation pheromone» by Ishay and Perna, 1979).
3. Use of scents as orientation cues. Wasps might then begin to search for scents when moving from an old to a new nest site, making the assembly pheromone begin to function as an orientation cue.
4. Short, directional recruitment trails. Selection could then favor nest foundresses that attract or lead potential joiners to their new nests by applying scent marks in the region between nests, as in *Mischocyttarus labiatus* (Litte, in press).
5. Long migration trails. New nest sites a long distance from the old nest could then be located via a series of scent marks forming a trail, as in the swarming Polybiini.

The advantages of swarming

Swarming has two salient consequences : long-distance migration, and large foundress groups. Migration away from the location of a damaged nest must sometimes enable wasps to escape a region frequented by predators or parasites, or some other unfavorable aspect of an abandoned site. And it would tend to reduce competition among the offspring of fissioning mature colonies. However, nothing is known about comparative colony success following different lengths of migration, since even the latter datum is very rarely obtained except for very short migrations. There is more basis for speculation regarding the advantage of a large foundress group. In *Polistes* multi-foundress colonies have better survival rates (Gibo, 1974) and higher productivity (Gibo, 1978 ; Metcalf and Whitt, 1977 ; Gamboa, 1978) than single-foundress nests. And in *Ropalidia marginata* the probability of extinction of colonies correlates negatively with the size of the adult population (Gadagkar et al., 1978). Furthermore, the larger the foundress group the quicker the establishment of large brood comb (West-Eberhard, 1969). The importance of quickly rearing a new crop of adults is dramatized by the high mortality rate (short life expectancy) of workers compared to the time required to replace them. In a colony of the swarming polybiine wasp *Metapolybia aztecoides* the average time required to rear a female from egg to first foraging (55 days) exceeded the foraging lifespan of workers (7-52 days) (West-Eberhard, 1978). Thus a new colony is in danger of running out of

workers (and going extinct) before new workers can be produced. I have documented the near extinction of a swarm-founded colony of *Synoeca surinama* due to worker mortality (West-Eberhard, 1981). Obviously, the larger the group of workers and queens present in the swarm, the more likely is the colony to survive a pre-elergence decline in adult numbers. Strassmann (in press) reached a similar conclusion in a study of the effects of group size in *Polistes*. She found that reduced probability of orphaned brood (and colony extinction) is a more important consequence of large adult population than defense against parasitoids and predators. The ability to swarm must contribute of the Polybiini in the tropics (Richards, 1971) where this and other adaptations (Jeanne, 1975) seem to enable colonies to survive despite frequent predation, especially by ants (see Jeanne, 1975 ; Chadab, 1979).

A COMMENT ON THE EVOLUTION OF SWARMING IN RELATION TO MATING SYSTEMS OF SOCIAL WASPS

It is a striking fact that the very little known about the behavior of tropical polybiine males indicates that they, like the females, are capable of following, and in some species making, scent trails. In the llanos orientales of Colombia (Meta) I observed *Polybia sericea* males abdomen dragging on certain leaves in a small (560 m^2) area of pasture. Four marked males repeatedly visited the same 75 dragged (presumably marked) leaves day after day for 16 days. Although I did not see mating in ten hours of observation, and foragers of the same species did not seem to react to the leaves visited by males, it seems likely that virgin queens seek such areas and mate there. Males of this species (and some others, e.g., *Polybia liliacea*) have a conspicuous medial depression in the terminal gastral sternite that I found lacking in males of *Parachartergus colobopterus* known to engage in a reproductive tactic not involving trail marking (see above). Similarly, Litte observed male abdomen dragging and patrolling sites in *Mischocyttarus flavitarsis* (Litte, 1979) and in *M. labiatus* (Litte, in press) the same species in which females abdomen drag «recruitment trails» between new and old nest sites. I have observed dragging and patrolling by males of *M. melanarius* (Cameron) and *M. mexicanus* (form *sternalis*) in Costa Rica (cf. Jeanne and Castellon, 1980, who report patrolling without dragging by males of *M. drewseni*). In *M. mexicanus* form *sternalis*, males have very long brushlike hairs on the overlapped margin of the terminal three sternites (most developed on the penultimate sternite) (cf. Litte, 1979 on *M. flavitarsis*, in which males have glands and hairs on sternites 5 and 6). These males return to the same leaves even after a lapse without marking of

more than two months, suggesting that their scent marks are very long lasting (mate attractant scent marks of honeybees last up to seven years – Butler, 1970). This raises the question of whether there is a connection between the scent trails of males and those of females. It is possible that polybiine male pheromone originated as chemical mimics of already attractive scents used by females in swarming ; or that sexual attractants evolved first and are simulated by swarming pheromones. On the other hand, trail marking could have evolved independently in the two contexts, or could have originated independently and been followed by convergence in the scents used by the two sexes. Abdomen dragging by males near newly founded nests occurs in the non-swarming wasp *Polistes canadensis* (pers. obs.), and I have also seen it by solitary eumenid males (a *Zethus* species) near active nesting holes. This indicates that at least the glandular apparatus for producing scents could have been present in males prior to the evolution of swarming by females. It would be of interest to compare the chemical structures of male and female sternal gland secretions. The only possible indication I have that the two sexes may react to the same scents is the observation of males present at very recently initiated nests (see above), raising at least the possibility that they followed the scent trail of the founding swarm. Some co-evolution of male and females pheromones in social wasps seems possible from the fact that there is much evidence in bees (in which this is a better studied aspect of social biology) for contextflexibility (and, hence, evolutionary lability) in the functions (or «meanings») of pheromones (e.g., see Michener, 1974).

A POSSIBLE RELATION OF INTRA-COLONY COMPETITION AND SWARMING IN BEES

As in *Metapolybia* wasps, reproductive swarming in *Apis mellifera* is preceded by dramatically increased reproductive competition among females, associated with the emergence of young gynes. In the case of honeybees, the timing of gyne production is regulated by a complex of factors (see Michener, 1974) and coincides with times of high worker population and a diminution in the production of queen substance (and, hence, presumably decreased suppression of queenlike tendencies in nestmates). As in *Metapolybia*, worker honeybees participate in the activities surrounding reproductive competition among queens. During the pre-swarming period of reduced foraging and egg-laying the queen «is often disturbed by workers forming a ball around her or striking her» (Michener, 1974, p. 132). And the younger and/or smaller among newly matured gynes are distinguished by the workers and killed (see Michener, 1974, p. 209). The possibility that older, larger gynes more successfully meet

challenges of «testing» workers (as is suggested by the queen selecting process in *Metapolybia* – see West-Eberhard, 1978) has apparently not been investigated in honeybees. «Piping» of honeybee queens seems to me likely to play a role in competition among gynes : it occurs only at times when there are, or recently have been *multiple* mature queens in a colony (Otis, 1980) ; and once a mature gyne has begun piping those emerging later move silently to the bottom of the hive where they are ignored by resident queen and workers (summary in Otis, 1980). If this interpretation of the function of piping is correct, the facts that piping and swarming are associated in honeybees (Michener, 1974 ; Otis, 1980), and that piping can even lead to swarming in colonies lacking other preparations for swarming (Simpson and Cherry, 1969 ; Simpson and Greenwood, 1974), further indicates that reproductive swarming of honeybees is associated with intra-colony reproductive competition. In honeybees, colonies are able to regulate the onset of competition among gynes (and, hence, the timing of swarming) by restricting the timing of gyne production. Honeybee swarming (colony fission) may originally have occurred as a function of competition among gynes, and then selection may have favored making this event coincide with periods of ample provisions and/ or crowding and perhaps other conditions (see Winston an Taylor, 1981) enhancing the probability of success of new colonies.

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EVOLUTION OF POLYETHISM IN ANTS :
OBSERVATIONAL RESULTS AND THEORIES

D. FRESNEAU, J. GARCIA PEREZ and P. JAISSON

Equipe de Recherche Associée au CNRS nº 885, Laboratoire d'Ethologie, Université Paris XIII, 93430 Villetaneuse, France

and

Centro de Investigaciones Ecológicas del Sureste, San Cristóbal de Las Casas, Chiapas, México

SUMMARY

Reports to date concerning social evolution in the family Formicidae leed us to distinguish the most primitive subfamilies (Ponerinae and Myrmeciinae) from the higher subfamilies (Myrmicinae, Formicinae and Dolichoderinae). Generally speaking, the most primitive subfamilies are characterized by some particular traits like reduced number of individuals by colony and a very slightly marked caste polymorphism. Conservely, societies in evolutioned subfamilies are generally constituted by a higher number of individuals, with more evident polymorphism. The question we tried to answer is if the taxonomic belonging to a subfamily (exepting particular cases of regressive evolution as social parasitism) is more representative of a higher level in social evolution than those characteristics of a society, concerning its size and the degree of caste polymorphism. This study was carried out by comparing to the genus *Neoponera* two other genus : a «primitive» one (*Ectatomma* : subfamily Ponerinae), and an «evolutioned» one (*Myrmecina* : subfamily Myrmicinae). In fact, *Ectatomma* constitutes relative important societies and presents a marked polymorphism between the queen and workers, while *Myrmecina* constitutes societies with a small number of individuals, characterized by slight morphological difference between the queen and workers. The study of ethograms and sociograms by using methods of data analysis led us to conclude that social characteristics (number of

individuals, polymorphism) might be better than the taxonomic criterion to appreciate the degree of social evolution of an ant genus.

RÉSUMÉ

La bibliographie actuelle concernant l'évolution sociale dans la famille Formicidae distingue classiquement les sous-familles primitives (Ponerinae et Myrmeciinae) des sous-familles les plus évoluées (Myrmicinae, Formicinae et Dolichoderinae). On admet généralement que les sous-familles les plus primitives sont caractérisées par des traits particuliers tels que le nombre réduit d'individus par colonie et un polymorphisme de caste peu marqué. Inversement, il est admis que les sociétés, dans les sous-familles évoluées, sont populeuses et présentent un polymorphisme de caste accentué. La question que nous nous sommes posée est de savoir si l'appartenance taxonomique à une sous-famille est un meilleur indice du degré d'évolution sociale que d'autres caractéristiques de la société, comme la taille ou le polymorphisme de caste (exception faite des cas particuliers d'évolution régressive comme le parasitisme social). Cette étude consiste à comparer le genre *Neoponera* (sous-famille Ponerinae) à deux autres genres : l'un «primitif», *Ectatomma* (sous-famille Ponerinae), l'autre «évolué», *Myrmecina* (sous-famille Myrmicinae). En fait *Ectatomma* présente des sociétés assez importantes et un polymorphisme marqué, tandis que *Myrmecina* présente des sociétés peu populeuses où le polymorphisme est faiblement marqué. L'examen des éthogrammes et des sociogrammes en recourant aux méthodes de l'analyse des données permet de conclure que les caractéristiques sociales (nombre d'individus et polymorphisme) peuvent être meilleures que les critères purement taxonomiques pour apprécier le degré d'évolution sociale d'un genre de fourmi.

INTRODUCTION

The work so far published concerning the phylogenetic organization of ants indicates that certain subfamilies are less evolved than others.The criteria used in making this distinction concern mainly morphological characteristics. The theorical reviews by Brown (1954 and 1960) are fairly representative of this approach. This leads to a classification in which the subfamily Ponerinae contains genera considered to be more primitive than those contained in the subfamily Myrmicinae. This statement must however be modified because within the Ponerinae subfamily there are different levels of evolution. The *Amblyopone* are for the moment considered to be the most primitive living genus. This has been confirmed by the study of those few fossil finds such as those of the ancestral ant *Sphecomyrma* (Wilson, Carpenter and Brown, 1967). Based on the anatomical characteristics of this fossil ant, these

authors haved proposed a phylogenetic organization of the Formicidae, based on two different directions of evolution developped :

1 – The «Poneroïd complex» includes, for example, the subfamilies Dorylinae, Pseudomyrmicinae and Myrmicinae. These later are considered to have developped from the Ponerinae. At the base of the complex, the *Amblyopone* represents the most primitive genus.

2 – The «Myrmecioïd complex», which includes the Dolichoderinae and Formicinae is thought to have devélopped from the primitive subfamily Myrmeciinae. The recent report by Taylor (1978) concerning the rediscovery of the fossil living ant *Nothomyrmecia macrops* suggests that important modifications are needed in this branch of evolution and leads the author to place the genus *Nothomyrmecia* at the base of the Myrmecioïd complex.

Much information concerning the biology of ant colonies shows appreciable differences between the species. For example, the *Amblyopone*, classed amongst the most primitive species, live in colonies with only a modest cast polymorphism between the queen and workers, as it was shown by Brown, Levieux and Gotwald (1970), Gotwald and Levieux (1972), Levieux (1972). On the other hand, the Myrmicinae, an evolved subfamily, found colonies with many individuals, in which cast polymorphism is very noticeable, see for example Wilson's review (1968). These factors should logically influence the social organization of labour (polyethism). It is now generally admitted that the division of labour is a function of both the age and size of the workers. We know that the young workers are most likely to be nurses whereas the old ones are foragers, as demonstrated for Myrmicinae by Buckingham (1911), Heyde (1924), Goetsh and Eisner (1930), Weir (1958) ; or for Formicinae by Buckingham (1911), Kiil (1934), Okland (1930), Otto (1958), Dobrzanska (1959). Polymorphism of workers also appears to have a determining role in task distribution. This difference in size is sometimes such that the workers are divided into subcasts of minors and medias for the nest (eg. Goetsh and Eisner, 1930, Weber, 1972, and Wilson, 1968). There appears also to be joint determinism by these two factors in a number of evolved species (Oster and Wilson, 1978).

Little is known about the social organization of «primitive» species. There is a suggestion of continuous polymorphism amongst the workers of certain species of *Myrmecia* (Wilson, 1971), whereas Bonavita and Poveda (1970) have noted the probable existence of age Polyethism (in the absence of polymorphism), in *Mesoponera cafraria*. We must reserve judgements on this issue, however, because Traniello (1978) has concluded that there is no age polyethism in the very primitive genera *Amblyopone pallipes*. Our aim is to utilize a new method to examine the social organization of three genera selected for their evolutionary affiliation within the poneroid complex. These

genera are caracterized by low numbers of individuals in each colony, which makes individual analysis possible. The genera we have studied are :

– *NEOPONERA* (subfamily Ponerinae) caracterized by polygyny (at least for the species studied) and the absence of clear polymorphism between queen and workers ;

– *MYRMECINA* (subfamily Myrmicinae), generally monogynous, caracterized by clear polymorphism (Baroni Urbani, 1968) ;

– *ECTATOMMA* (subfamily Ponerinae). According to Wilson, Carpenter and Brown (1955), this genus is the most advanced of the Ponerinae because they consider the tribe Ectatommini to be the ancestors of Myrmicinae. Since Taylor's recent suggestions (1978) do not call this affiliation into question, we will attempt to test the value of this hierarchy from the point of view of social organization.

METHODS

After collection, each society was installed in the same type of artificial nest. It consisted of a nest made of plaster maintained in the dark, and an artificially lighted foraging area. Each member of the colony was marked with small number, easy to identify during observations (Fresneau and Charpin, 1977).

An observation consists of noting the location and activity of each ant at the moment it is identified. The observation is finished when all members of the society have been identified and scored. It takes between 5 and 20 minutes for this operation, depending of the size of the colony. The observation is repeated 8 to a 10 times per day over a period of 7 to 12 days. This procedure allows one to establish a schema of the activities of each of the individual members of the society during the same period of time. After the observational period, the results of the scoring were summed for each individual, which allows one to reconstruct the social activity of the colony ; it also constitutes a sufficiently rich data set to establish a social ethogram or sociogram. In this respect, we have the same goal as Wilson (1973) in his study of *Zacryptocerus varians*. Our method, based on individual analysis, allows us both to establish the repertoire of behavioural acts of the species and the distribution of the individual roles around these activities. To this end, we have used a different mathematical treatement from that used by Wilson. Our data are particulary suited to the «correspondances factorial analysis» method, described by Benzecri et al. (1973). This method has previously been used in the study of ants by Lenoir and Mardon (1978) in *Lasius niger* placed in a test situation. In the present context, this test and the use of taxonomic analysis method allow us to produce a simplified but rigorous picture of the social organization of a colony in a normal situation (Fresneau and Dupuy, in preparation).

This purely descriptive technique gives no information concerning the variability that could result from testing a sample of colonies ; one must therefore be careful not to overgeneralize the results. This test, however, constitutes a useful basis for the subsequent analysis of strictly quantitative data that are presently being collected. For this reason, we have chosen to present for each species the results of a typical colony from the sample of colonies so far observed, while taking into account the factors highlighted by the results of all the colonies so far analysed.

RESULTS

First species : Neoponera fœtida

This species is restricted to the neotropical forests. All the societies studied were collected in different areas of the Lacandon forest in Chiapas state, Mexico. One frequently observes polygyny, or at least the integration of winged females (out of six colonies collected only one was monogynous). The colony for which we will report the results included seven wingless females. Their dissection after the observational period revealed that three of them were inseminated. There were also 57 workers, 15 larvae, 8 cocoons and eggs. Sixty sets of observations recorded over eight days thus resulted in a total of 3840 individual scores. These observations allowed us to establish 36 behavioural categories distributed between the nest and the foraging area. In order to facilitate subsequent comparisons, however, we pooled together those categories which were highly correlated in the factorial analysis ; for example, the category «care of eggs» combines licking and transport of eggs, and the category «care of larvae», combines licking, transporting and feeding larvae. The results we report do not therefore constitute an ethogram of the behavioural categories, but a slightly simplified grid of 24 behaviours which highlights the social role existing in the society. Benzecri's correspondances factorial analysis allowed us to produce figure 1, which simplifies the relationships between the behaviours on the one hand and the individual ants on the other. At a subsequent stage, one may establish the correspondance between these two groups of variables and verify the social roles.

The analysis based on the behaviour. In figure 1, the two axes shown are those which most effectively classify the data. Each of them represents a continuum between two extremes ; thus, axis F1 (the horizontal axis or factor 1) allows the separation of two groups of behaviours :
– behaviours concerning care of the brood (especially care of eggs) are found at the negative end of this axis.
– a varied set of behaviours, all situated in the foraging area, constituting the

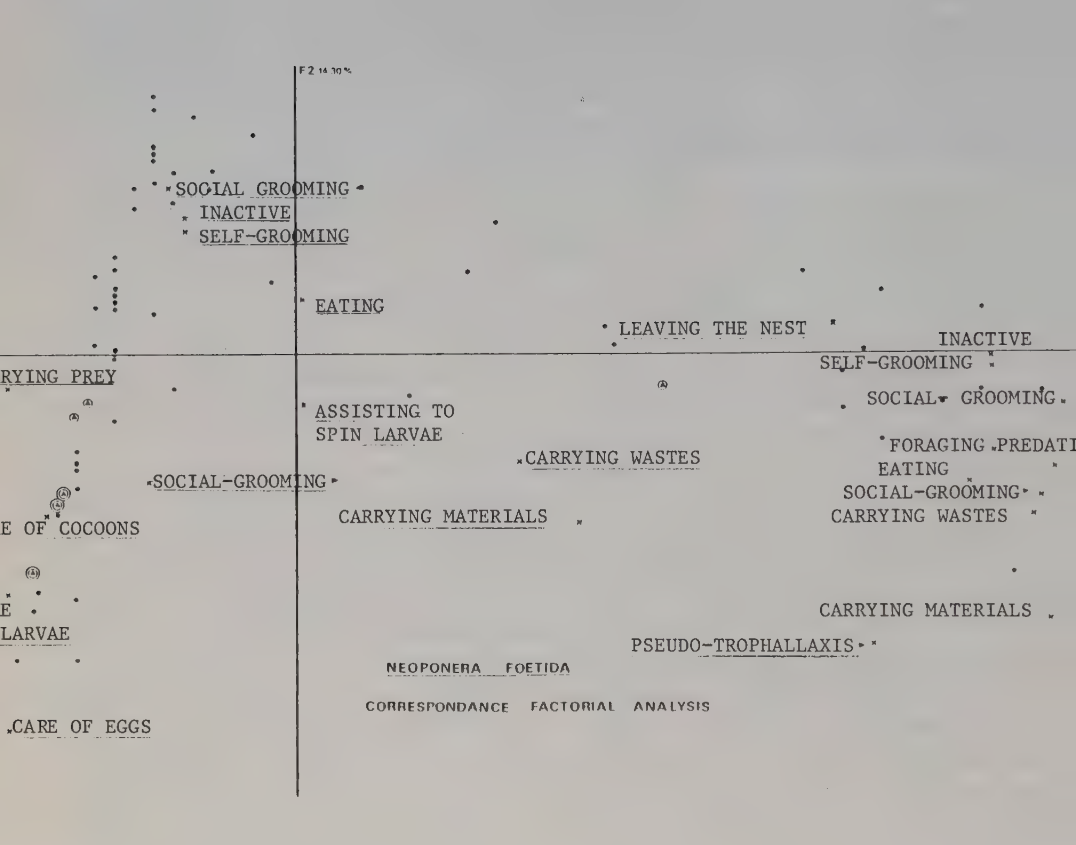


Fig. 1 – Graphic representation of 24 behavioural categories within the framework of the first two axes. Ⓐ queens (3) ; Ⓐ females (4) ; ● workers (57). The underlined activities (e.g. self-grooming) are activities performed inside the nest. The behaviour not underlined are the outside activities. An arrow → indicates an instigator of that social behaviour. An arrow ← indicates a recipiant of that social behaviour.

Fig. 1 – Représentation des 2 premiers axes. 64 individus, 24 comportements. Ⓐ reines (3) ; Ⓐ femelles (4) ; ● ouvrières (57). Les comportements soulignés sont situés dans le nid (ex. : «self-grooming») les mêmes comportements non soulignés ont été observés à l'extérieur du nid. Les comportements sociaux comportant une flèche → désignent le fait d'être actif ou donneur dans cette interaction. La flèche ← indique le fait d'être passif ou receveur.

outside tasks of the society, especially food supply. These behaviours are found at the positive end of this axis.

This first continuum «represents» or «explains» 38,5 % of the total variance of the data. The axis F 2 (vertical axis or factor II) represents 14 % of the total variance. It contrasts the behaviours concerning the care of the brood, at the negative end, with the set of activities located outside the nest, at the positive end (such as inactivity, feeding, self-grooming, etc.). This set represents the activities common to all the ants and we have called them non-specific activities, in contrast to those activities previously separated by axis F 1. These behaviours are quantitatively significant and represent the «center of gravity» of the social structure of *Neoponera*, which can be summarized by the existence of three extremes : a) care of brood ; b) non specific behaviours in the nest ; c) the outside tasks supplying provisions.

Certain other classes of behaviour are categorized separately. These are the domestic tasks which include the transport of the material needed by the larvae for spinning the cocoon, as well as tidying and transferring waste or the remains of prey. One may observe these behaviours either inside the nest (underlined) or outside (not underlined). In figure 1, these behaviours occupy an intermediate position between non specific activities and the outside tasks. In fact, the domestic tasks are characterized by the axis F 3, which clearly separates them from all the other activities. They are, however, close to the non specific activities. The domestic tasks are in general quantitatively unimportant, and axis F 3 represents only 10 % of the total variance. For simplicity this axis has not been shown on the figure. The same applies to the 20 other axes, which each represents very little of the total variance (less than 3 %). We do not report them here.

Analysis based on individuals. The distribution of the ants (shown as black dots or triangles) is very similar to the organization of activities and show clear polyethism. One can assume that two ants that are close on the figure have a similar behavioural profile. At the same time, the proximity of individuals to each extreme allow one to assume (provided certain precautions are taken) a correspondance between the two sets of variables. For example, the data points found near the «care of eggs» section represent a group of ants who are strongly characterized by that behaviour. On the other hand, these ants are a long way from the outside tasks : they never engage in these behaviours. One may distinguish another class of ants characterized by «non specific» activities, and a further class which engages predominantly in predation and foraging. As a result, figure 1 gives a picture of the behavioural profile of each ant, and allows one to describe the relationships between behaviours. It is however not easy to clearly delimit those groups that are specialized in one task. A complementary analysis allow us to treat this

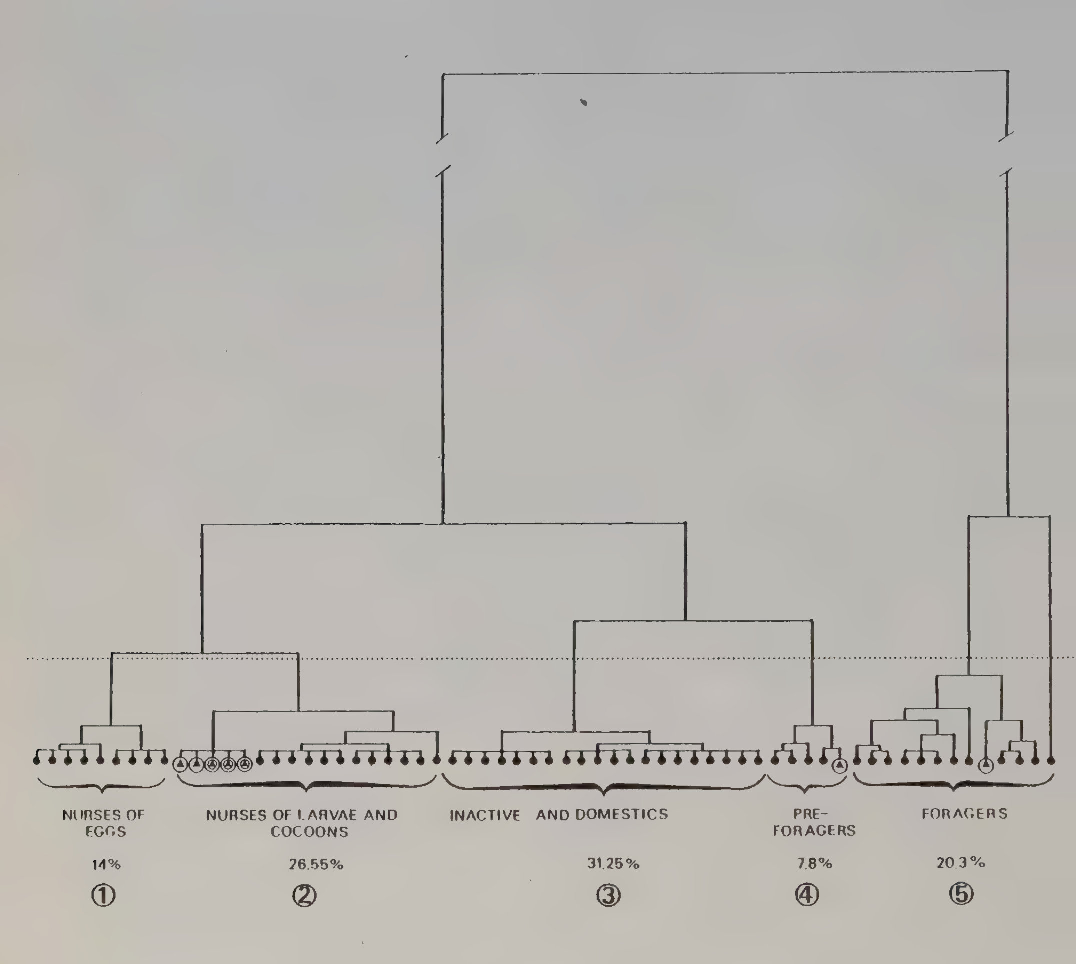


Fig. 2 – Hierarchical Cluster Analysis : dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. queens ; infertilized females ; ● workers.

Fig. 2 – Analyse de classification hiérarchique. Dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. reines ; femelles non fécondées ; ● ouvrières.

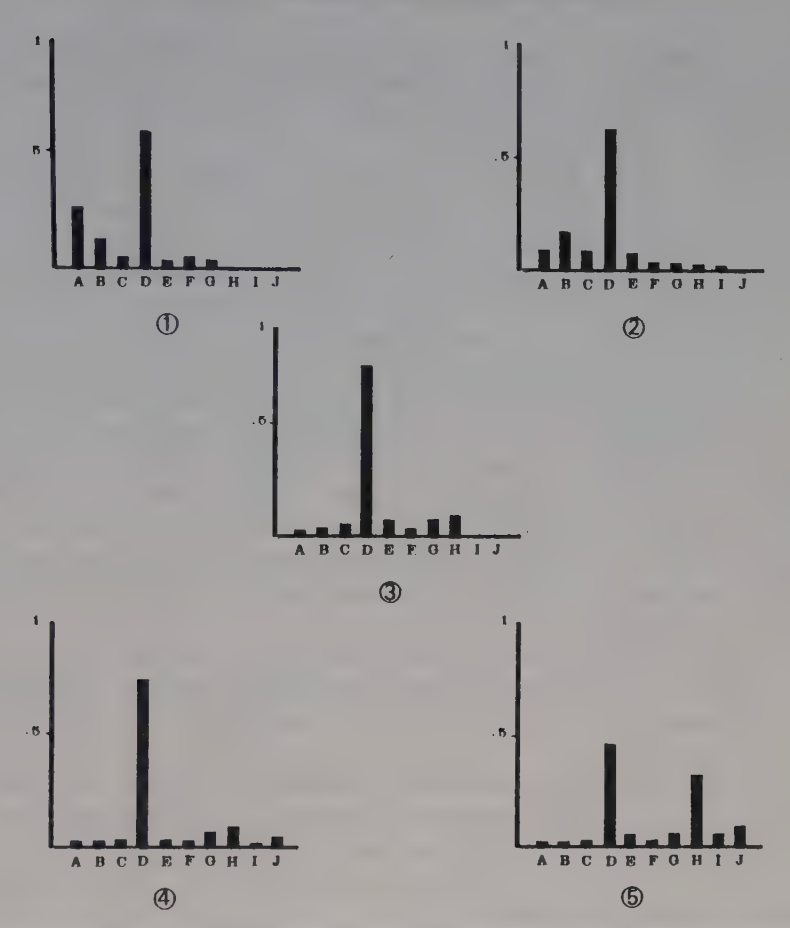


Fig. 3 – Behavioural profile for each group defined by the dendrogram. For convenience we have grouped the behaviour into 10 categories : A – care of eggs ; B – care of larvae and assisting larvae to spin ; C – care of cocoons ; D – non specific activities in the nest : inactive, self-grooming, eating ; E – social grooming →inside and outside the nest ; F – social grooming ←inside and outside the nest ; G – domestic activities in the nest : carrying of materials, carrying wastes, carrying prey, transporting liquids and pseudo-trophallaxis ; H – non specific activities outside the nest : leaving the nest, foraging, self-grooming, eating ; I – domestic activities outside : carrying materials and carrying of wastes ; J – supply : predatory behaviour, carrying prey and transporting liquids. The height of the bars represents the relative frequencies in each class of activity over the total number of activities shown by the group.

Fig. 3 – Profils comportementaux des groupes isolés par le dendrogramme. Afin de faciliter les comparaisons nous nous sommes limités à 10 activités : A – soin des œufs ; B – soins des larves et assistance au tissage du cocon ; C – soin des cocons ; D – activités non spécifiques dans le nid ; E – toilettes sociales →dans et hors du nid ; F – toilettes sociales ←dans et hors du nid ; G – activités domestiques dans le nid : transport des déchets, des matériaux, des proies et pseudotrophallaxies ; H – activités non spécifiques hors du nid : quitter le nid, exploration, toilette individuelle, manger ; I – activités domestiques à l'extérieur : transport des matériaux et des déchets ; J – approvisionnement : chasse, transport des liquides. Les valeurs des graphiques représentent les fréquences relatives de chaque classe de comportement sur le total d'activités présenté par le groupe.

question : it is based on automatic classification techniques or cluster analysis. This consists of grouping together individuals as a function of the similarity of their behavioural profiles. We have used an ascending hierarchical classification based on the distances of X^2.

Figure 2 shows the set of clusters for the ants of this colony. The distance between individuals or groups of individuals represents their degree of similarity. A short distance indicates a considerable resemblance, a long distance indicates little resemblance or even an opposition between the elements connected. This is the case, for example, between the ants in group 1 to 4, and those of group 5. Two further pairs of groups may be dissociated : 1 and 2 on the one hand, and 3 and 4 on the other. A higher level of analysis allows one to distinguish each of the five groups. It seems reasonable to limit the analysis to a significant degree of similarity (indicated here by the dotted line). Beyond that, interpretation becomes fragmented and approaches the continuous distribution obtained in figure 1. When this limit is used, the classification permits to separate five groups of ants. The roles played by them may be appreciated by calculating, for each group, the relative frequency of each behaviour over the total of all behaviours of the five groups, for ten categories of activity (Fig. 3) :

– Group 1 includes the workers dedicated to the care of the brood. Their nursing activities are primarily directed towards the eggs (f = .20 the highest frequency recorded this type of caring behaviour). We have named the ants of this group egg-nurses.

– Group 2 includes three queens, two unfertilized females and 12 workers. Their level of non-specific activities is higher than in the preceding group (f = .55), and they care for the cocoons (f = .21) and the larvae (f = .12). However, they assume little care for the eggs (f = .03), which are cared for exclusively by the ants of group 1.

– Group 3 contains workers with no apparent role ; they are characterized by a high level of non-specific activities (f = .85). We have called them «inactive» because of their low level of involvement in the ergonomic tasks described in figure 1.

– Group 4 contains four workers and a unfertilized female. These ants are relatively inactive in the nest, apart from various transport tasks, but they explore the foraging area for most of the waste removal from the nest to the exterior.

– Group 5 finally, contains 12 workers and a unfertilized female specialized in foraging (f = .55). They provide food for the society (f = .20), and display little behaviour towards the brood.

One individual is placed separately on the right of the graph : this is a worker specialized in the transport within the nest, of material that

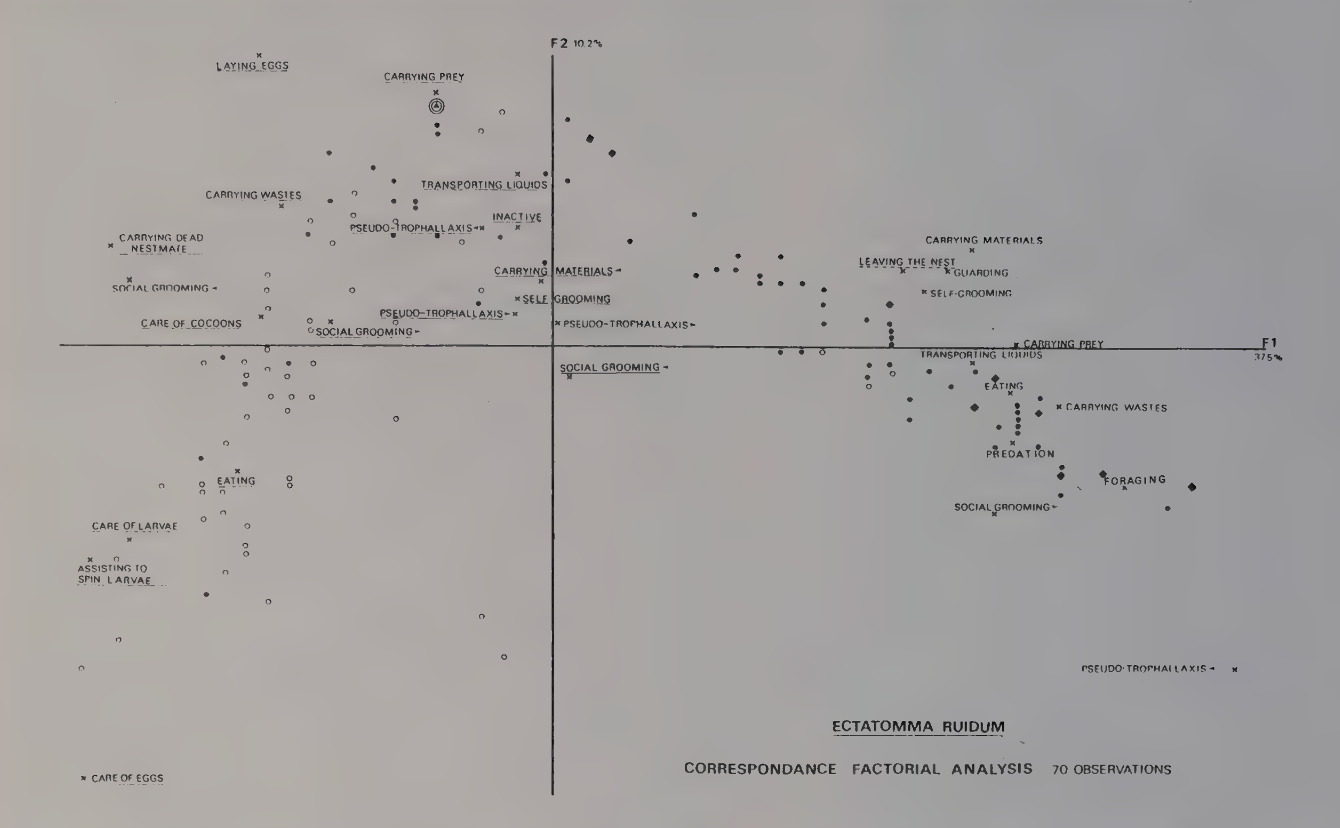


Fig. 4 – Graphic representation of 31 behavior types within the framework of the first two axes 127 individuals. (▲) queen (1) ; ○ young workers (49) ; ● mature workers (68) ; ◆ dead workers (9).

Fig. 4 – Représentation graphique des 2 premiers axes : 127 individus, 31 comportements. (▲) reine (1) ; ○ jeunes ouvrières (49) ; ● ouvrières adultes (68) ; ◆ ouvrières mortes (9).

subsequently serves as a support for the spinning larvae. This result has also been obtained for a close species, *Neoponera apicalis* (Fresneau and Dupuy, in preparation). As a result of this information, figure 3 shows a very clear distinction between the behavioural profiles of those ants that remain most of the time inside the nest (Group 1 to 4) and those that supply provision (Group 5). Among the sedentary ants, two sets may be distinguished : the nurses, and those ants, without a particular role, who deal with the domestic tasks. We thus again demonstrate the three poles described in the correspondance analysis. The presence of queens and the unfertilized females amongst the nurses, and the presence of the other unfertilized females in the last two groups demonstrates the remarkable integration of the unfertilized females in the division of labour. It is not an isolated case, because we have observed unfertilized females participating in food-supply in a natural setting. We consider that this is a distinctive feature of the *Neoponera*.

Second species : Ectatomma ruidum

This neotropical species lives in open biotopes. The colonies were collected near Tuxtla Gutierrez, Chiapas, Mexico. The society we present here included one queen, 126 workers, eggs, larvae and cocoons. The colony was observed 70 times, which revealed a broarder behavioural repertoire. This included a «guarding» function and more frequent pseudotrophallaxis. This latter consists of transporting droplets of sugary liquids between the mandibles, and «giving» them to other workers in the foraging area, or in the nest, (the *Neoponera*, prefer to transport fruit fragments directly into the nest). Figure 4 shows the repertoire of 31 behavioural classes projected onto the first two axes of the factorial analysis. The axis F 1 (or first factor) represents 37 % of the total variance. As in the previous cases, it contrasts the activities in the foraging area (not underlined), with those in the nest (underlined). Amongst the latter, care of the eggs is located at the negative pole of axis F 1. The second axis (F 2) represents 10 % of the total variance and separates inactivity in the nest (at the positive end) from care of eggs and larvae (at the negative end). However, egg-laying and receiving pseudotrophallaxis are perfectly characterized by the third axis (F 3), which represents 4,8 % of the variance. This axis strongly contrasts these behaviours with all of the others, and especially care of eggs. It seems that this axis is representative of the queen's activity. The fourth axis (F 4) represents 4 % of the variance. Within the nest, it contrasts care of cocoons with care of eggs and larvae. Outside the nest, it clearly separates predatory behaviour and food supply from waste disposal and the transport of material. Summarizing, the ethogram for *Ectatomma ruidum* seems broadly similar to the organization

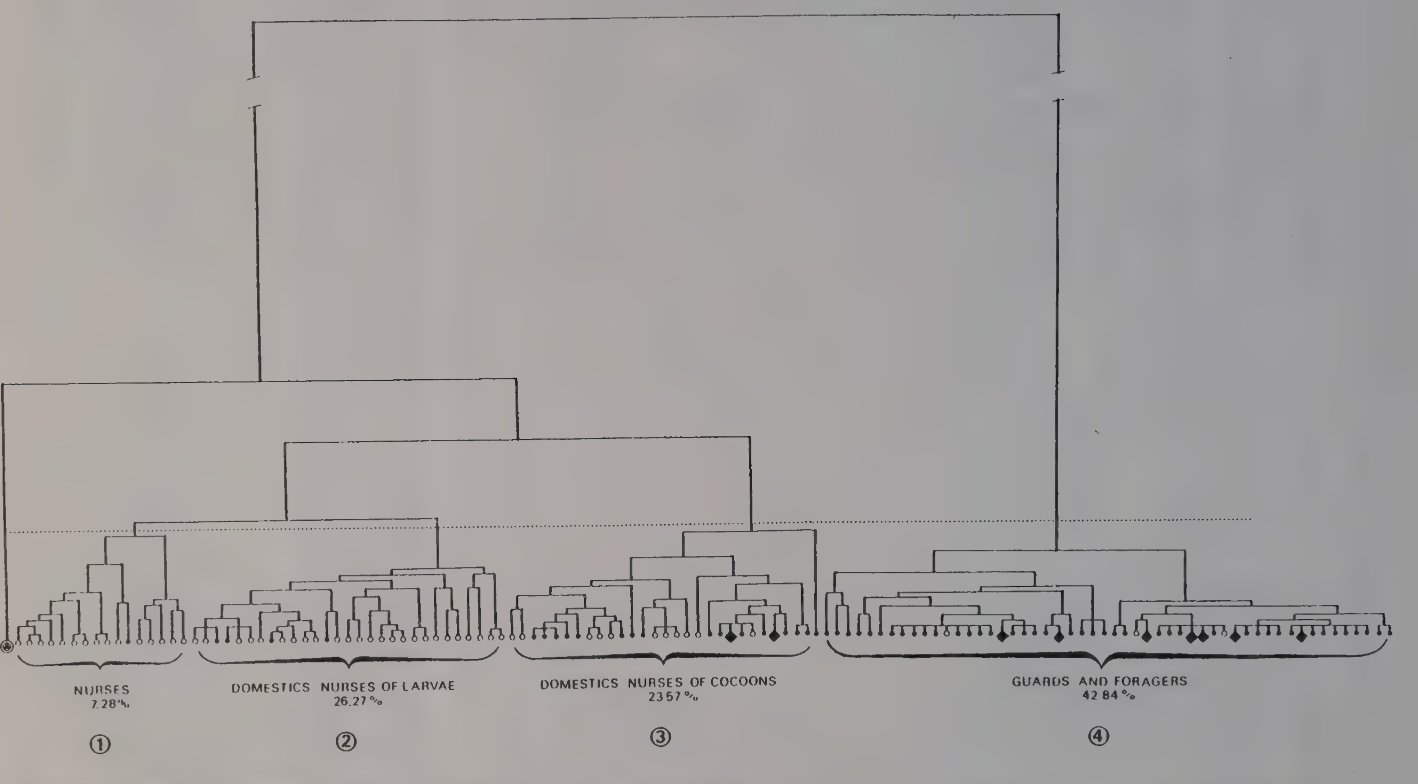


Fig. 5 – Hierarchical Cluster Analysis : Dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. ▲ queen ; ○ young workers ; ● matures workers ; ◆ dead workers.

Fig. 5 – Analyse de classification hiérarchique : dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. ▲ reine ; ○ jeunes ouvrières ; ● ouvrières adultes ; ◆0 ouvrières mortes.

described for *Neoponera*. Three primary poles control the activities of the colony :

– The food supply outside the nest and all those activities situated in the foraging area, including guarding the nest entrance.

– Non specific activities within the nest, combined with domestic tasks and the care of cocoons.

– Care of the eggs and larvae, dissociated from the second pole, and constituting the exclusive activities of the nurses.

The distribution of the ants is perfectly continuous between the three poles. The young workers, aged between 8 days and 1 month during the observational period, are represented by open circles on the graph. These circles are massively grouped around the nursing and non specific activities in the nest. After an examination of the individual cases, it appears that the youngest are significantly specialized in the care of the larvae, but we also observe some in non specific activities and even guarding of the nest entrance. The adult workers (identified by filled circles), at least 1 month old during the observation period, are divided between non specific activities and outside tasks ; few of them are nurses. Nine workers, identified by black diamonds, died during the observation period ; their position amongst the outside tasks indicates that ants spend more and more time outside the nest at the end of their lives. Polyethism related to age is therefore highly probable.

The queen is located near the non specific activities. In *Ectatomma ruidum* she is above all inactive. Confinated to the egg chamber, she remains very passive receiving pseudotrophallaxis from the workers. She is, in fact, characterized by the axis F 3 (not shown here), associated with egg-laying and receiving pseudotrophallaxis. The taxonomic analysis shown in figure 5 clarifies and confirms the preceeding remarks, separating four groups of individuals :

– Group 1, consisting of 16 workers (of which 15 are young), is characterized by nursing activities (see figure 6). These are furthermore the only ants to care for the eggs (f = .10). As opposed to *Neoponera*, the low level of care for the eggs suggests that for *Ectatomma* the eggs require little attention from the workers.

– Group 2, containing 29 workers (of which 23 are young), is characterized by care of the larvae (f = .22).

– Group 3, also contains 29 individuals of all ages (only 11 young). This group distinguishes itself by care of cocoons (f = .60) and provides little care of eggs (f = .006) or of larvae (f = .08). For this reason, group 3 is clearly separated from the first two on figure 5.

– Group 4, is quantitatively the largest (52 workers of which 3 are young), and is distinct from the 3 other groups. The behavioural profile reveals that

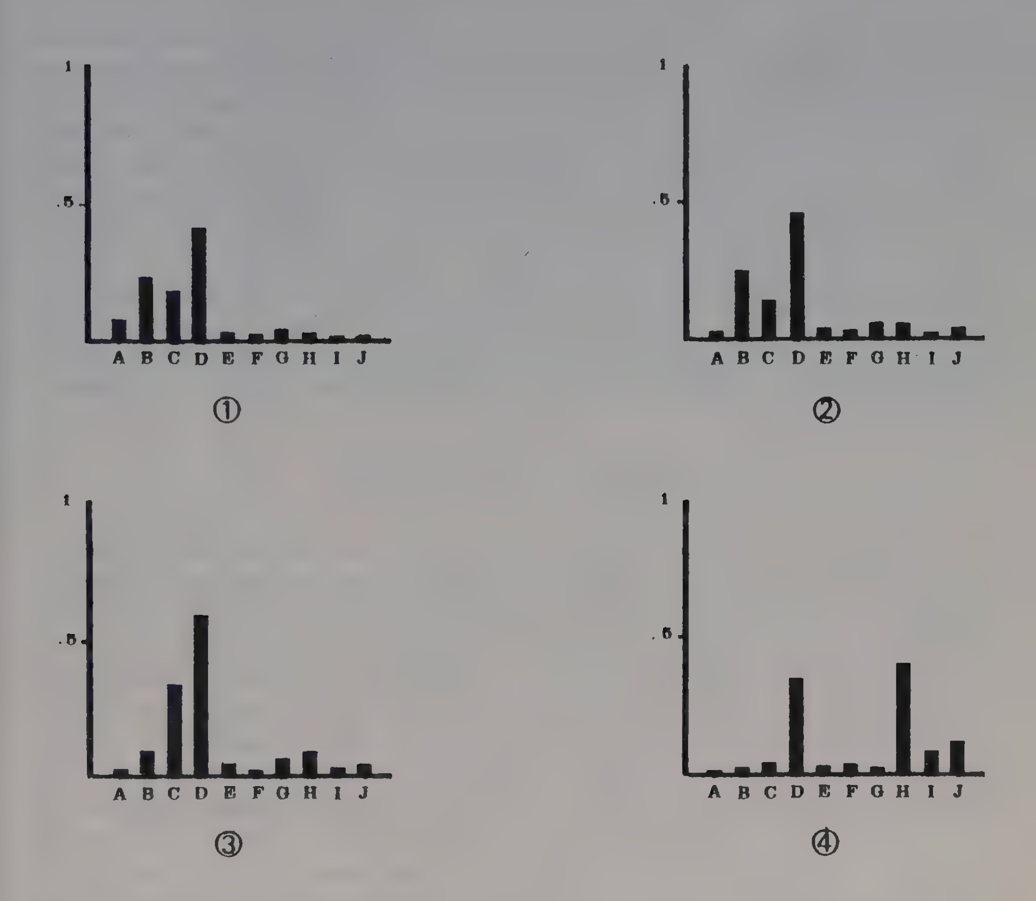


Fig. 6 — Behavioural profile for each group defined by the dendrogram. A — care of eggs ; B — care of larvae and assisting larvae to spin ; C — care of cocoons ; D — non specific activities in the nest : inactive, self-grooming, eating ; E — social grooming → inside and outside the nest ; F — social grooming ← inside and outside the nest ; G — domestic activities in the nest : carrying of materials, carrying wastes, carrying prey, transporting liquids and pseudo-trophallaxis ; H — non specific activities outside the nest : leaving the nest, foraging, self-grooming, eating ; I — domestic activities outside : carrying materials and carrying wastes ; J — supply : predatory-behaviour, carrying prey and transporting liquids.

Fig. 6 — Profils comportementaux des groupes isolés par le dendrogramme. A — soin des œufs ; B — soin des larves et assistance au tissage du cocon ; C — soin des cocons ; D — activités non-spécifiques dans le nid : inactivité, toilette individuelle, manger ; E — toilette sociale → dans et hors du nid ; F — toilette sociale ← dans et hors du nid ; G — activités domestiques dans le nid : transport des matériaux, des déchets, des mortes ; H — activités non-spécifiques hors du nid : exploration, quitter le nid, toilette individuelle, manger et garde hors du nid ; I — activités domestiques : transport des matériaux, transport des ordures, transport des mortes ; J — approvisionnement : prédation, transport des proies, transport des liquides et pseudo-trophallaxies.

the outside activities are well represented : this foraging group includes up to 50 % of the members of the colony. This proportion, which was observed with other colonies, may constitutes a characteristic trait of *Ectatomma*.

The queen is logically categorized separately because she does not participate in the main activities of the society, but is connected to the set of ants that rarely, if ever, leave the nest. This result is notably different from that we obtained for *Neoponera*, and the non-integration of the queen in the social activity seems to characterize *E. ruidum*. We must also note the existence of a complex polyethism related to age. In this organizational system, the three types of brood are separated according to a model which Wilson (1976) has termed «temporal continous caste system», in which sensitivity and responsiveness of the ants to stimulation evolues progressively with age.

Third species : Myrmecina graminicola

Although this paleartic species belongs to the evolved subfamily Myrmicinae, polymorphism is less pronounced than in *E. ruidum* and the number of individuals in the observed colonies is also typically much less than for *Ectatomma*. The colony presented here was collected near les Eyzies, Dordogne, France. During the observation period it consisted of 1 queen, 52 workers of which 21 were less than 10 days old, eggs, 20 larvae and 4 nymphs. Ninety observations were taken over a 12 days period. The ethogram is slightly different from the previous species, and we never observed predation. It seems that the food supply occurs in an episodic manner (only twice during the observational period, whereas food was available in the foraging area). When the food supply does take place, a short but massive recruitment of the members of the colony occurs, and trophallactic exchanges become widespread. Constantly, one or two foragers wander about close to the nest entrance, where one or two guards remain immobile and beat with their antennae any individual trying to enter. Similarly, there is a guard, within the nest, at the entrance of the chamber containing the queen and the brood. In this species, the nymphs are naked and copiously licked, as are the large larvae. The eggs and small larvae are licked much less, and are often covered by totally immobile nurses. Sometimes they are isolated from the floor by the nurses, who suspend them in bunches between their legs, and by the queen, who helps with this task. All of these activities (protection, transport, licking) have been regrouped according to the type of brood, in order to facilitate comparisons with the previous species. The ethogram is represented on fig. 7.

Axis F 1 (37,5 % of the total variance) clearly contrasts the outside activities (at the positive end) with the care of the brood (negative end).

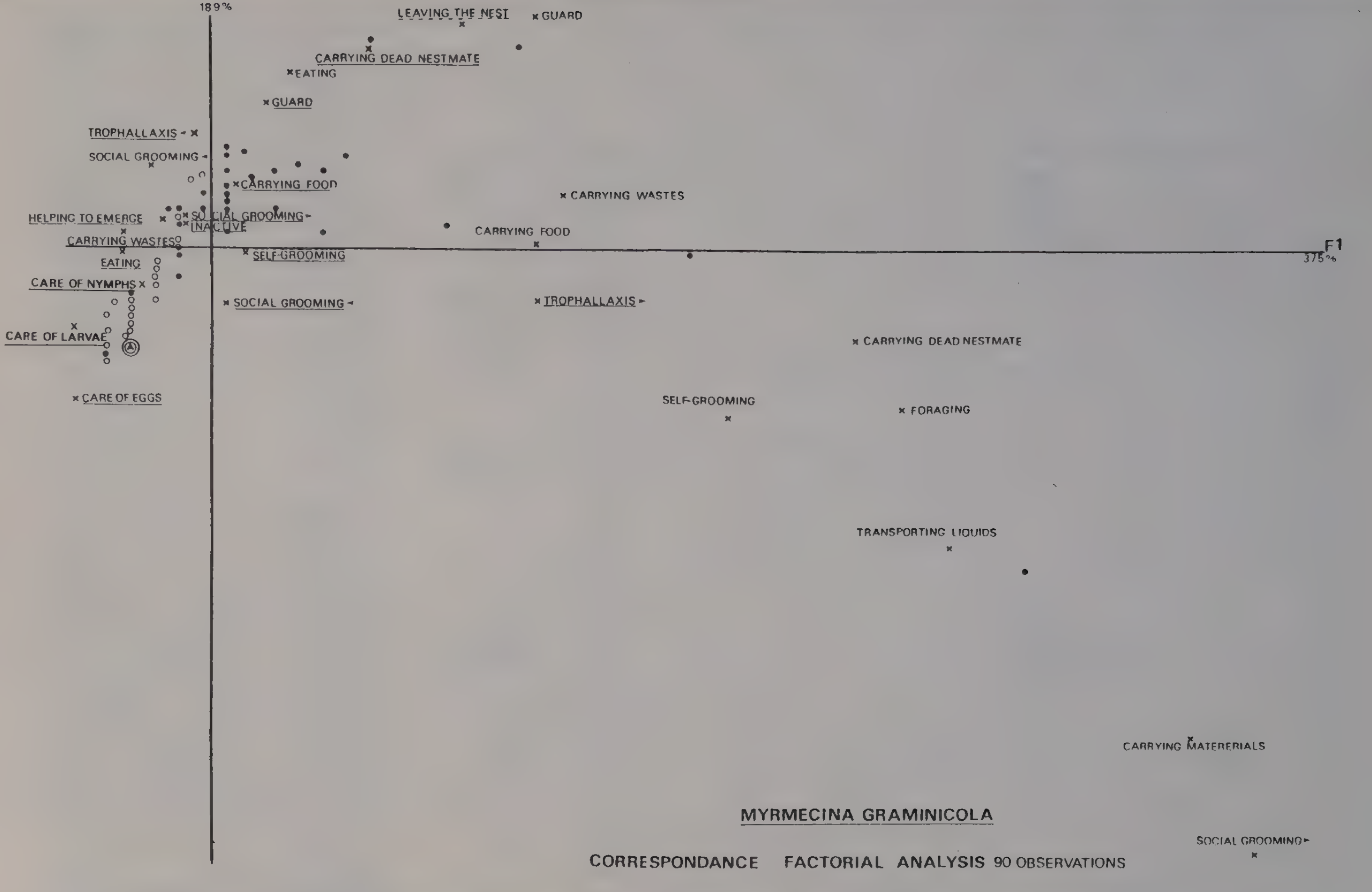


Fig. 7 — Graphic representation of 28 behavioral categories whitin the framework of the first two axes. 52 individuals (▲) queen (1) ; ○ young workers (21) ; ● mature workers (30).

Fig. 7 — Représentation deux premiers axes. 52 individus, 28 comportements. (▲) reine (1) ; ○ jeunes ouvrières (21) ; ● ouvrières adultes.

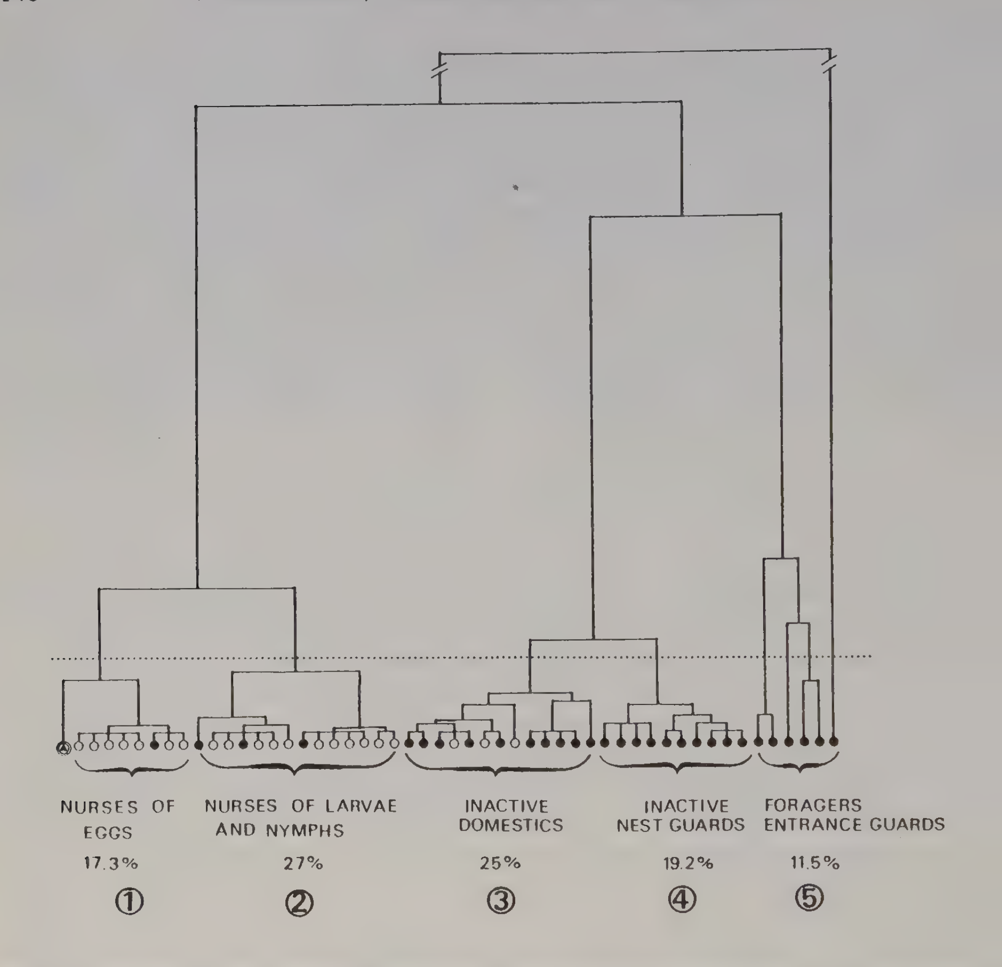


Fig. 8 – Hierachical Cluster Analysis. Dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. ⓐ queen ; ○ young workers ; ● mature workers.

Fig. 8 – Analyse de classification hierarchique : dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. ⓐ reine ; ○ jeunes ouvrières ; ● ouvrières adultes.

It must be emphasized that foraging and domestic activities are the only significant outside tasks.

The axis F 2 (18 % of the total variance) contrasts outside domestic tasks with nonspecific activities in the nest and, to a lesser degree, care of eggs. The non-specific activity pole also contains nest-guarding behaviour and the act of leaving the nest. Finally, food supply is also located near this pole, which implies that the food supply is done by a significant proportion of the

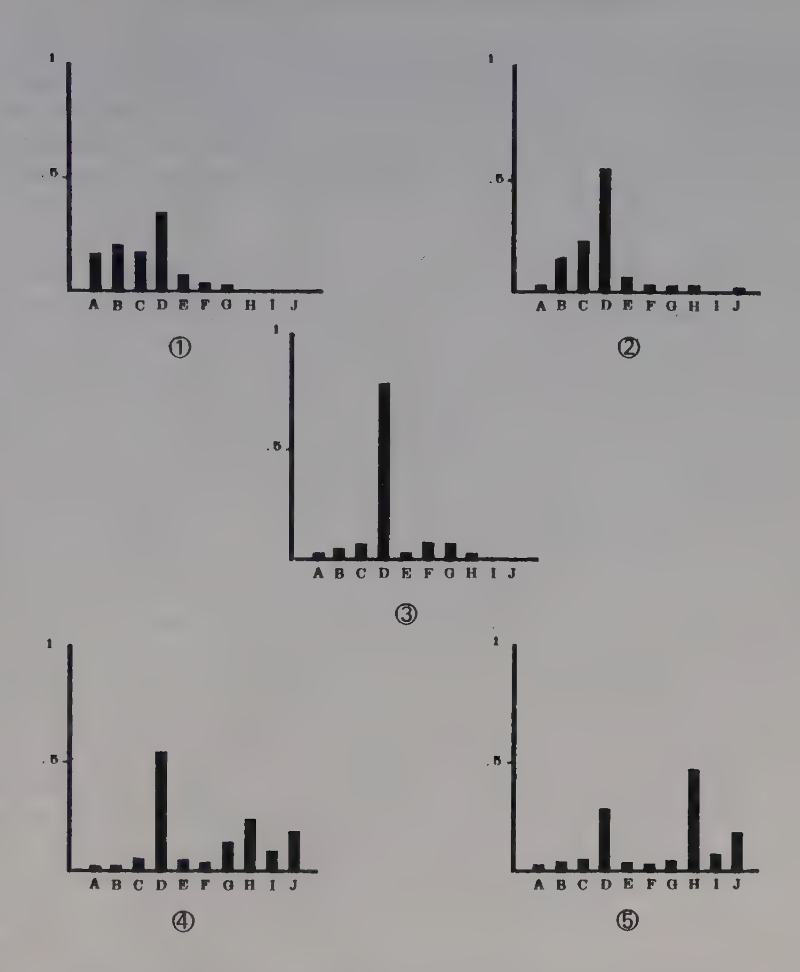


Fig. 9 — Behavioral profile for group defined by the dendrogram. A — care of eggs ; B — care of larvae ; C — care of nymphs and assitance to emerge ; D — non specific activities in the nest : inactive, self-grooming, eating and guarding inside the nest ; E — social grooming → inside and outside the nest ; F — social grooming ← inside and outside the nest ; G — domestic activities in the nest : carrying materials, carrying wastes, carrying dead nest-mate ; H — non specific activities outside : foraging, leaving the nest, self-grooming, eating, guarding ; I — domestic activities outside : carrying materials, carrying wastes, carrying dead nest-mate ; J — supply : carrying food, transporting liquids and trophallaxis.

Fig. 9 — Profils comportementaux des groupes isolés par le dendrogramme. A — soin des œufs ; B — soin des larves ; C —soin des nymphes et soins lors de l'éclosion ; D — activités non spécifiques dans le nid : toilette individuelle, manger, garde de l'entrée de la chambre aux œufs ; E — toilette sociale → dans et hors du nid ; F — toilette sociale ← dans et hors du nid ; G — activités domestiques dans le nid : transport de matériaux, des déchets et des mortes ; H — activités non spécifiques hors du nid : exploration, quitter le nid, toilette individuelle, manger et garder ; I — activités domestiques hors du nid : transport de matériaux, des déchets et des mortes ; J — approvisionnement : transport de nourriture et des liquides, trophallaxies.

domestic workers, or those that are inactive in the nest. This function could occur in an episodic manner after a recruitment initiated by the foragers.

The axis F 3 (11 % of the variance, and not shown here) dissassociates «leaving the nest» and «guarding the entrance» with the nest of the non-specific activities. Axis F 4 (5 % of the variance) contrasts the care of eggs with the care of larvae and nymphs, which corresponds to a similar organization to that of *E. ruidum*.

The distribution of individual ants on figure 7 closely follows the organization of activities. The young workers are massively grouped around the nursing activities ; the queen is integrated with this group, being an egg-nurse. The older workers are spread out between the non-specific activities and the outside tasks. The taxonomic analysis, represented on figure 8, confirms and refires this categorization : virtually, all the young workers (18 out of 21) are found in the first two groups. Group 1 contains the queen and the egg-nurses. Group 2 includes the nurses of larvae and nymphs, that we could separate as two subgroup, as with *E. ruidum*, but the degree of specialization is less pronounced. The rest of the colony includes the workers engaged in non-specific activities in the nest, guarding and foraging. Among the foragers (group 5) a worker which permanently explores the foraging area is set appart ; if we combine this ant with the guards, it appears that only 11 % of the members of the colony usually explore outside the nest. This low proportion (also obtained in another colony) is notably different from *E. ruidum*, in which half the colony is permanently outside the nest.

To summarize, it appears that the *Myrmecina* constitute limited societies in which all the workers spend most of the time in the nest. This increases their unobtrusiveness in the field, while the episodic character of the food supply implies the massive distinction in the cluster of figure 8 between the nurses (groups 1 and 2) and the rest of the colony. Figure 9 confirms and explains this dichotomy : groups 1 and 2 present behavioural profiles which are very similary to those of individual nurses (the same level of inactivity is observed in both cases, f = .55), but a difference is that group 1 preferentially cares for the eggs (f = .27), whereas group 2 directs its nursing activity (f = .83), principally the domestic tasks. It would therefore be reasonable to assume that these two groups constitute a reserve that can be called upon for a short time to forage. This is especially the case for groups 4, which shows a higher level of «leaving the nest». The last group (5), less homogenous, is characterized by non-specific activities outside the nest (foraging and guarding the nest entrance, f = .45), and domestic tasks that are always outside (f = .12). The foraging is part of the behavioural repertoire of these workers. At the appropriate time, these workers, which spend most of their time outside, locate the food and then recruit the inactive workers in the nest. The low level

Table I — Behavioural profile of queens belonging to three species studied. Relative frequencies of activities displayed by the queens over the observational period.

Tableau I — Profils comportementaux des reines appartenant aux trois espèces étudiées. Fréquences relatives des activités présentées par les reines sur le total d'observations effectuées.

	Care of Eggs	Care of Larvae	Care of Cocoons	"Non-specific" Activities	Social-grooming	Trophallaxis	Egg-laying	Total
NEOPONERA FOETIDA 3 ♀, 60 Obs.	.058	.222	.362	.350	.006	–	–	1
ECTATOMMA RUIDUM 1 ♀, 70 Obs.	.030	.007	–	.856	.077	–	.030	1
MYRMECINA GRAMINICOLA 1 ♀, 90 Obs.	.306	.031	.006	.544	.094	.019	–	1

of foraging unfortunately prevented us from quantitatively studying this recruitment behaviour. After *Neoponera* and *Ectatomma*, the organization of *Myrmecina* constitutes a third original solution. The main points to be remembered are the integration of the queen in the care of the eggs, and the innovation of the significant function of foraging to a section of the inactive workers.

DISCUSSION

Is it possible to establish an evolutionary hierarchy based on polyethism, as a result of proceding analysis ?

Many limiting factors make it difficult. First of all, it is possible that the descriptive analysis used does not account for the total behavioural repertory of each species. Certain distinct but in frequent activities could have eluded our investigation due to the observational method used. Perhaps by extending this research, we could in the future, to pool the results of several colonies into the same factorial analysis. This would increase our chances of observing the influence of these rare behaviours. A new systematization for each species could then be drawn up. On the other hand, it would be useful to complete and enlarge the set of evolutionary levels studied by carrying out similar studies on other species selected on the basis of recent taxonomic findings. This diversification of the levels of investigation would permit a more coherent interpretation of the results. Three levels of investigation therefore constitute a minimal initial sample. Partial results reveal a considerable stability in polyethical organization. Summarizing, in all cases the division of labour is based on three poles of inactivity : nursing towards the brood (in the nest), non-specific activities common to all ants (in the nest) and the activities that occur outside the nest. The domestic tasks, both inside and outside the nest, are spread between the second and third poles. The distribution of individuals between these poles is always perfectly continuous. This characteristic must be very wide spread amongst the social Hymenoptera, because Brothers and Michener (1974) came to the same conclusion for semi-social colonies of primitive bees.

On the basis of the results we have reported here, *Neoponera* represents the most primitive reference point, with the ants being divided equally between the three poles, although the foragers are nevertheless the smallest group. The *Myrmecina* have a broadly similar organization to the *Neoponera* (the same proportion of nurses) and there are even fewer foragers. In both species many inactive individuals constitute a reserve available according to the needs of the society. In the case of *Myrmecina*, for example, the inovation of recruitment

permits a restricted number of foragers to recruit, if necessary, the normally inactive sedentary ants, for the provision of a massive and rapid food supply. The case of *Ectatomma* is somewhat different, because the permanent foragers constitute the largest group. As opposed to the preceding species, the societies are more populous and the organization of labour is both less adaptable and more specialized. The absence of recruitment in a populous society with and abundant brood could explain the permanent investment in a large number of foragers. The size of the societies and the ability to recruit would therefore be key elements in the social organization.

In an earlier study the integration of unfertilized females into the social roles of the species *Neoponera apicalis*, was demonstrated (Fresneau and Dupuy, in preparation), and we report here the same thing in *Neoponera foetida*. Furthermore, subequent dissection allowed us to identify which of these females were fertilized. Here, it seems possible to compare the behavioural profiles of the queens of the three species. The results are shown in table 1, in which the main valves are framed. Generally, the queens play no role in the domestic and outside tasks. In each case, however, they show a much higher level of inactivity and non-specific activities than the workers. The participation of the queens in the division of labour concerns principally the care of the brood. For example, the queens of *Neoponera* spread their nursing activities accross the eggs, larvae and cocoons, whereas the queen of *Myrmecina* preferentially cares for the eggs and the small larvae. The *Ectatomma* queen, the most passive, is submitted to intensive grooming by the workers. It is the only queen that we have observed ovipositing, and from the behavioural point of view, the *Ectatomma* queen strongly resembles the queens of evolved species, who are totally dedicated to egg-laying, abandoning the other behaviours in which they engage during the foundation of the colony. On the other hand, it is frequently considered that the Ponerine queens continue their nursing activities in the adult society (Le Masne, 1953). Thus, the level of the queen'inactivity, or alternatively, her role in the care of the brood, would be a good indication of the species'evolutionary level. In this respect, *Ectatomma* would be placed at the top of the classification of these three species, *Neoponera* the bottom, and *Myrmecina* paradoxically in an intermediate position. We have attempted to test the value of this classification by studying the degree of polymorphism of the three genera reported here. Two biometric indices were used : the width of the head (between the eyes) and the maximum length of the thorax.

The measures were taken from a fairly large sample of females and workers coming from all the colonies reared in the laboratory. Then, we established a relationship between the workers and females. The results, portrayed in table 2, show that the same type of categorization is obtained on

Table II – Estimation of polymorphism between castes in the three species studied. The biometric measurements were obtained from samples obtained in various colonies.

Tableau II – Profils comportementaux des reines appartenant aux trois espèces étudiées. Fréquences relatives des activités présentées par les reines sur le total d'observations effectuées.

Species	Caste		HEAD Interocular width (mm)	THORAX Prothoracic width (mm)
NEOPONERA FOETIDA	♀ (7)	$\overline{X}$	2.145	1.761
	☿ (57)	$\overline{X}$	2.040	1.445
	♀/☿		1.052	1.219
ECTATOMMA RUIDUM	♀ (2)	$\overline{X}$	3.00	2.780
	☿ (46)	$\overline{X}$	1.960	1.450
	♀/☿		1.531	1.917
MYRMECINA GRAMINICOLA	♀ (4)	$\overline{X}$	0.860	0.700
	☿ (46)	$\overline{X}$	0.738	0.460
	♀/☿		1.165	1.521

the basis of both types of biometric index. Low values indicate little polymorphic difference (near to 1), which is the case for *Neoponera*, and for many Ponerine species and in general for the «primitive» species. On the other hand, higher values reflect a pronounced polymorphism. This is the case for *Ectatomma*, whereas *Myrmecina* yields intermediate values, which are closer to those of *Neoponera* than to those of *Ectatomma*.

Although belonging to the subfamily Myrmicinae, *Myrmecina graminicola* form societies in which there is little difference between queen and workers either behaviourally or morphologically. The paradoxical position of *Myrmecina graminicola* in the hierarchy is confirmed by these two results. One may therefore assume that the polymorphic separation between queens and workers is also a good indication of the polyethic separation of the castes. This is slight in the primitive species, but not noticiable for the evolved species. In this respect *E. ruidum* should be considered to be a highly advanced Ponerine. It would be useful, in the future, to extend this analysis to a broader sample of species in order to more completely test the value of this relationship. We know that caste polymorphism is a good indicator of the level of socialization and this feature can be generalized to all the social Hymenoptera (Michener, 1974 ; Lin and Michener, 1972). Thus, social evolution tends to radically separate the queen caste, which is concerned with reproduction, from the worker caste which deals only with the trophic function of reproductive assistance. This process is at work in the ants, and appears very early in their evolution, although we must admit that it is not spread in a homogenous way accross all the sub-families (Wilson, 1953). This evolutive process of separation, which can be objectively judged at the morphological level, can be correlatively observed at the behavioural level and by the degree of integration of the queen into the social roles.

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EVOLUTION ET RÔLE DES COMMUNICATIONS ANTENNAIRES CHEZ LES INSECTES SOCIAUX

A. LENOIR* et P. JAISSON

Equipe de Recherche Associée au C.N.R.S. n° 885,
Université Paris XIII, Avenue J.B. Clément, 93430 Villetaneuse, France

RÉSUMÉ

Les communications antennaires existent dans tous les groupes d'insectes sociaux. Elles sont importantes dans tous les aspects de la vie sociale : reconnaissance, alarme, recrutement des congénères pour l'exploitation d'une source alimentaire ou l'émigration, et trophallaxies. Les communications antennaires sont basées sur des schèmes moteurs simples : des battements antennaires sur les congénères. La bibliographie nous permet de distinguer deux aspects principaux de l'évolution de ces communications :

– Chez les Formicidae, des séquences comportementales hautement stéréotypées, appelées «comportement d'invitation», sont associées durant le phénomène de recrutement à des phéromones de piste. Le comportement d'invitation est efficace à lui seul uniquement chez quelques espèces de Ponerinae. Chez les espèces qui utilisent le recrutement chimique de masse, le comportement d'invitation semble subsister à l'état de relique. Il est possible de trouver différents degrés d'évolution à l'intérieur d'un même genre (*Camponotus* par exemple).

– Durant la trophallaxie, les battements antennaires sont associés à des mouvements des pattes antérieures dans la stimulation mécanique des congénères. La stimulation antennaire est également utilisée pour traire des Aphides ou solliciter des larves ; elle est mimée par des myrmécophiles. Chez les fourmis et les abeilles la stimulation tactile est plus ou moins facultative tandis que chez les guêpes des rituels complets sont associés à une compétition sociale.

* Adresse postale : Laboratoire d'Ethologie et de Psychophysiologie – Faculté des Sciences – Parc de Grandmont – 37200 TOURS, France.

En conclusion, les connaissances actuelles sur l'analyse séquentielle des mouvements antennaires peuvent difficilement être utilisées pour en tirer une information sur le niveau phylogénétique des différentes espèces d'insectes sociaux.

SUMMARY

Evolution and role of the antennal communications in social insects

Antennal communications are present in all groups of social insects. They are very important in several aspects of social life : recognition, alarm, recruitment of nestmates for exploitation of a food source or emigration, food-exchange through trophallaxis. Antennal communications are based on simple motor patterns : antennal beatings on the nestmates. The litterature concerning this problem leads us to distinguish two main aspects of evolution :

– In Formicidae, during recruitment phenomena, highly sterotyped behavioral sequences called «invitation behaviour» are associated with trail pheromones. Invitation behaviour is effective alone only in some species of the Ponerinae. In some species which use chemical mass recruitment, invitation behaviour seems to be a relic. We find several degrees of evolution in the same genera (for ex. *Camponotus*).

– During trophallaxis, antennal beatings are associated with movements of the forelegs, for mechanical stimulation of the nestmates. Antennal stimulation is also used for milking aphids or sollicitation of larvae, and it is mimed by myrmecophiles. In ants and bees tactile stimulation is more or less optional whereas in wasps complete rituals are associated with social competition.

In conclusion the sequential analysis of antennal movements cannot yet be used to obtain information on the phylogenetic level of the different social insect species.

INTRODUCTION

Un des aspects les plus spectaculaires du comportement des Insectes sociaux est certainement le «langage antennaire» découvert chez les fourmis par Huber en 1810 (p. 176). Pour André (1885, p. 63) «le toucher antennal parait donc être le mode principal de conversation employé par nos insectes». Un auteur aussi sérieux que Forel écrit : «C'est par ce moyen qu'elles traduisent à leurs compagnes leurs sentiments, leurs découvertes, leurs alarmes, leurs intentions, etc.» (1922, III p. 68). Wasmann (1899) a le premier entrepris une étude systématique et a reconnu 10 situations où un animal oriente un congénère sur un objet ou une activité particulière à l'aide de battements antennaires. Les communications antennaires reposent sur des organes sensoriels répartis

sur les antennes et sur toute la surface du corps. Les récepteurs antennaires sont bien connus (voir par exemple les revues de Slifer, 1961 et Schneider, 1964) et chez les insectes sociaux on reconnait au moins 4 fonctions sensorielles : chémoréception, mécanoréception, perception de la gravité, hygroréception. Les études électrophysiologiques portant sur l'olfaction sont nombreuses : Boistel, 1953 ; Boistel et col., 1956 ; Kaissling et Renner, 1968, pour l'abeille, Masson et Friggi, 1971 ; Masson et coll., 1974, chez la fourmi. Les recherches portant sur l'effet de stimulations tactiles sont beaucoup plus rares (Masson et coll., 1974 chez la fourmi).

Nous présentons ici une revue du rôle des communications antennaires et les caractéristiques de l'évolution de cette forme de communication au niveau des relations interindividuelles, du comportement d'invitation et des échanges de nourriture.

RELATIONS INTERINDIVIDUELLES

La reconnaissance interindividuelle chez les Insectes Sociaux peut s'effectuer à courte distance, mais s'accompagne souvent d'exploration antennaire réciproque, en face à face, pouvant durer plusieurs secondes. On en trouvera une description chez *Dolichoderus* (Torossian, 1973a). Ce comportement existe aussi chez les insectes sub-sociaux lors de la rencontre des partenaires sexuels, par exemple chez *Labidura* (Vancassel et Caussanel, 1968). Le face à face est parfois accompagné chez de nombreuses espèces de fourmis, de tressautements de l'ensemble du corps, dont la signification est complètement inconnue. Wilson appelle ce comportement «jittering» chez *Zacryptocerus varians* où il s'accompagne souvent de léchages et régurgitations (1976). Chez certaines Myrmicines, Wilson (ibid) décrit aussi un comportement particulier : les fourmis se tiennent face à face, le corps rigide, les antennes pointées vers la congénère avec quelques contacts antennaires. Ce comportement, dont le rôle est inconnu, est décrit maintenant chez de nombreuses espèces de diverses familles (Corn, 1980 ; Cole, 1980). Chez les guêpes, les battements antennaires traduisent le statut social des individus : ils sont réservés à la dominante, la dominée maintenant ses antennes serrées et immobiles. Ces contacts antennaires sont souvent le prélude d'une trophallaxie dans laquelle la dominée est donneuse (revue de Richards, 1971, p. 509).

Chez *Myrmecocystus*, Hölldobler a décrit en 1976 un comportement très particulier : il s'agit de tournois ritualisés entre ouvrières hostiles de colonies différentes. Ces tournois, qui durent 10 à 30 secondes, comprennent tout d'abord un face à face, puis une présentation latérale avec élévation du gastre et les fourmis tambourinent simultanément l'abdomen de l'autre avec

leurs antennes. Ceci représente le seul contact physique entre les deux fourmis, et le tournoi cesse quand l'une d'elles abandonne. Ces tournois peuvent conduirent à l'esclavagisme de la colonie la plus faible pour ce comportement.

Chez l'abeille on a longtemps considéré que la substance royale était transmise par léchage de la reine puis par trophallaxie. En fait il semblerait, d'après un travail récent de Seeley (1979) que les échanges alimentaires soient secondaires, la transmission se faisant surtout par contacts antennaires, avec des ouvrières «messagères» qui dispersent la substance royale dans la colonie. On vient de découvrir une phéromone inhibitrice de la ponte des ouvrières chez les fourmis (Berndt, 1977 et Passera, 1978), la distribution en est peut-être réalisée de la même manière que chez les abeilles.

COMPORTEMENT D'INVITATION

Il s'agit de séquences comportementales très stéréotypées et régulièrement utilisées par les fourmis dans des situations précises. Le comportement d'invitation permet les phénomènes de recrutement : pour explorer une nouvelle aire de récolte et exploiter une source de nourriture, pour transporter une congénère, pour déménager ou défendre la colonie. Le terme de comportement d'invitation semble avoir été utilisé pour la première fois par Hölldobler et coll. en 1974 (p. 112). Les séquences comprennent des battements antennaires de la tête ou du corps entier, et parfois des prises par les mandibules. Dans la plupart des cas, il y a simultanément des signaux chimiques : l'odeur de la nourriture pour un recrutement alimentaire, ou émission de phéromones. On verra que l'importance respective des signaux chimiques et du signal tactile est variable. Quand on a découvert les premières phéromones des insectes sociaux (Wilson, 1962), on a eu tendance à négliger le message tactile au profit du message chimique. En réalité on s'est aperçu que d'autres facteurs intervenaient. On a classé les comportements d'invitation en fonction de l'importance respective des signaux tactiles et chimiques :

Course en tandem (tandem-running) : il s'agit de la forme de recrutement la plus primitive puisqu'elle permet le recrutement d'une seule fourmi à la fois. L'ouvrière qui rentre au nid martèle sa congénère avec des mouvements de va-et-vient vers l'avant («jerking»), elle l'agrippe à la tête par ses mandibules et la tire en arrière puis se retourne. La fourmi recrutée garde le contact avec le leader par ses antennes. Aux signaux tactiles s'ajoutent des phéromones de surface. Chez les Ponérines, il ne semble pas y avoir de dépôt de trace par le leader : *Bothroponera tesserinoda* (Möglich, 1973 ; Maschwitz et coll., 1974), *Neoponera fœtida*, (Jaisson et Fresneau, 1978), *Neoponera apicalis* (observation inédite réalisée à l'aide de films) et au moins chez

2 espèces de Myrmicines du genre *Cardiocondyla* (Wilson, 1959). Une situation plus complexe est réalisée chez *Camponotus sericeus* (Hölldobler et coll., 1974) où la recruteuse associe le dépôt d'une trace émise par l'intestin postérieur au comportement d'invitation. La trace sert uniquement à l'orientation, le comportement d'invitation seul permet la mise en place du tandem. Il se présente de manière différente selon le type de recrutement : pour un recrutement alimentaire, au jerking, s'ajoutent des courses courtes avec offres de nourriture. Le jerking simple aboutit à un tandem running ou à un transport. Chez *Camponotus paria* le contact n'est pas nécessaire et la fourmi leader n'attend pas la suiveuse qui s'oriente avec la trace (Hingston, 1929 in Wilson, 1971, p. 249).

Chez 3 espèces de *Leptothorax*, Möglich et coll. (1974), puis Lane (1977) ont mis en évidence un comportement tout à fait particulier : la pourvoyeuse, après une ou plusieurs trophallaxies dans le nid, lève son gastre et émet une goutte de liquide en sortant son aiguillon. Ce comportement de «tandem calling» a un effet attractif sur les congénères et un tandem running démarre avec la première arrivée. Le comportement d'invitation disparait complètement au profit d'un signal chimique dont Möglich (1980) a montré qu'il provenait de la glande à poison. Le «tandem calling» a été retrouvé chez les Myrmicines esclavagistes comme *Harpagoxenus sublaevis* (Bushinger et Winter, 1977). La plupart de ces fourmis pratiquent d'ailleurs le tandem. Il en est de même chez *H. canadensis* et *Chalepoxenus* (Bushinger et coll., 1980).

Le comportement de «tandem calling» pourrait avoir une origine commune avec l'appel sexuel caractéristique des femelles de nombreuses espèces de parasites ou esclavagistes : *Harpagoxenus* (Bushinger, 1968 ; Bushinger et Alloway, 1979), *Leptothorax* (Bushinger, 1975), que l'on retrouve chez *Xenomyrmex* (Hölldobler, 1971b) et même chez les Ponérines *Amblyopone* et *Rhytidoponera* (Haskins, 1978). Chez *Rossomyrmex proformicarium*, espèce primitive de formicine esclavagiste, les ouvrières transportent individuellement leurs congénères dans le nid à piller, ce qui a la même efficacité que des tandems successifs (in Bushinger et coll., 1980).

Chez les abeilles *Lasioglossum* il existe un comportement voisin du tandem running appelé «backing et following» permettant de diriger les ouvrières chargées de pollen vers les cellules à approvisionner (Breed et Gamboa, 1977), et on retrouve le tandem-running chez les termites *Trinervitermes* (Leuthold, 1975).

Le recrutement de groupe. On parlera de groupe lorsque une exploratrice recrute des congénères qui sortent en formant un groupe plus ou moins important, la fourmi exploratrice en devenant le leader. Chez *Camponotus socius* le comportement d'invitation est associé au dépôt d'une trace de l'intestin postérieur et de la glande à poison. La trace indique la direction mais

ne peut pas, à elle seule, induire le recrutement, la fourmi leader doit être devant pour que le groupe progresse (Hölldobler, 1971a). Le comportement d'invitation est comme dans le cas précédent, différencié : des mouvements latéraux (waggle dance) pour le recrutement alimentaire et des mouvements d'avant en arrière (jerking) pour l'émigration. Le comportement de *Camponotus compressus* semble s'apparenter à celui de *C. socius* (Hingston, 1929, in Wilson, 1971, p. 249). Le recrutement de groupe est pratiqué aussi par diverses espèces de Myrmicines : lors d'un déménagement chez *Myrmica rubra* (Abraham et Pasteels, 1977) ou au début d'un recrutement alimentaire chez *Tetramorium caespitum* (Verhaeghe, 1977) et 4 espèces de *Myrmica* (Cammaerts, 1977 et 1980 ; Cammaerts et Cammaerts, 1980 ; Dlussky et coll., 1978). Quand il s'agit d'approvisionner la colonie, le recrutement évolue rapidement vers un recrutement de masse. Le recrutement de groupe existe aussi chez certaines fourmis esclavagistes lors des raids, avec un dépôt d'une trace : *Harpagoxenus americanus, Leptothorax duloticus, Epimyrma* et *Raptiformica* (Alloway, 1979 ; Bushinger et coll., 1980). Les diverses espèces de *Leptothorax* esclaves peuvent suivre aussi bien des tandems (voir plus haut) que des pistes de groupe. Chez *Aphaenogaster subterranea* on trouve aussi un recrutement de groupe mais la trace est utilisée seulement à l'obscurité. Les fourmis recrutées par le comportement d'invitation sont capables de trouver la nourriture sans trace ni leader (Voltzit, 1979).

Certaines espèces de Ponérines prédatrices de termites effectuent des raids en colonnes. Le leader est nécessaire chez *Leptogenys kitteli* (Baroni-Urbani, 1973) où il peut conduire des groupes allant au maximum à 60 individus, il n'est pas nécessaire chez *L. chinensis* (Maschwitz et Schönegge, 1977). Chez *Megaponera* les exploratrices sont plus nombreuses et la colonne comporte un grand nombre d'ouvrières ; le leader étant nécessaire dans certains biotopes (Longhurst et Howse, 1979) alors qu'il ne l'est plus lorsque les proies (termites) sont abondantes (Lévieux, 1966). On arrive dans ce cas au recrutement de masse. Pour toutes ces espèces de Ponérines, le rôle exact du comportement d'invitation est mal connu, Maschwitz et Mühlenberg (1975) pensent même que les signaux tactiles sont inutiles chez *Leptogenys ocellifera* ; pour cette raison on a porté un point d'interrogation sur la figure 1.

Le recrutement de masse, qui permet la sortie d'un grand nombre d'individus, est pratiqué chez de nombreuses espèces. Il est toujours associé à un signal chimique dont l'importance varie.

– Pour certaines espèces, seules les ouvrières activées par l'invitation de la recruteuse (jerking) suivent la piste. Le leader n'est pas nécessaire comme dans le recrutement de groupe. C'est le cas de *Formica fusca* (Möglich et Hölldobler, 1975), *Myrmecocystus mimicus* (Hölldobler, 1976b).

– Le comportement d'invitation permet une efficacité plus grande de la trace pour d'autres espèces : *Monomorium* (Sudd, 1957 ; Szlep et Jacobi, 1967), *Crematogaster* (Leuthold, 1968), *Camponotus pensylvanicus* (Traniello, 1977), *Eciton* (Chadab et Rettenmeyer, 1975), *Neivamyrmex* (Topoff et Mirenda, 1978). On retrouve ce phénomène chez les Termites *Zootermopsis* (Howse, 1965).

– Enfin le comportement d'invitation peut ne plus avoir de rôle important ni d'effet supplémentaire par rapport à la trace. On a alors un véritable recrutement de masse chimique. On l'observera chez *Solenopsis* (Wilson, 1962), *Lasius fuliginosus* (Hangartner, 1967), *Pogonomyrmex* (Hölldobler, 1976a) et *Atta cephalotes* (Jaffe et Howse, 1979). Au laboratoire le fait de déposer la phéromone de trace à l'entrée du nid suffit à induire la sortie de nombreuses fourmis.

– Pour certaines espèces les données sont moins claires. Chez *Pheidole militicida* Hölldobler et Möglich (1980) observent des pistes avec une phéromone provenant de la glande à poison, servant de signal de recrutement, mais les repères visuels sont importants dans l'orientation des ouvrières. Les auteurs ne peuvent indiquer le rôle éventuel des invitations pratiquées dans le nid. Le cas de *Pheidole pallidula* est controversé : pour Szlep-Fessel (1970) il s'apparente au type *Monomorium* (efficacité plus grande de la trace grâce à l'invitation) mais pour Couret (1978, p. 8) il n'existe pas de trace chimique chez cette espèce : les ouvrières recrutées sortent sans ordre apparent et trouvent la nourriture par une succession d'essais et d'erreurs. Chez *Tapinoma* et *Iridomyrmex* les auteurs accordent une importance plus ou moins grande au signal tactile : pour Szlep et Jacobi (1967) il augmente l'efficacité de la trace alors que pour Couret et Passera (1979) la phéromone suffit à elle seule. Des expériences complémentaires seraient nécessaires pour toutes ces espèces.

– Les fourmis esclavagistes du genre *Polyergus* pratiquent le recrutement de masse avec un comportement d'invitation très marqué et une phéromone de piste sauf peut-être chez *P. rufescens* (Bushinger et coll., 1980).

EVOLUTION DU COMPORTEMENT D'INVITATION (Fig. 1)

Le comportement d'invitation se présente sous la forme de séquences relativement simples et stéréotypées que l'on retrouvera avec des variantes selon les groupes. Il s'agit toujours d'interactions antennaires associées pour la recruteuse à une danse frétillante qui s'accomplit en courant vers le nid. Elle comporte des mouvements saccadés latéraux «waggling» ou d'avant en arrière «jerking», parfois verticaux, de la tête et du thorax ou même du corps

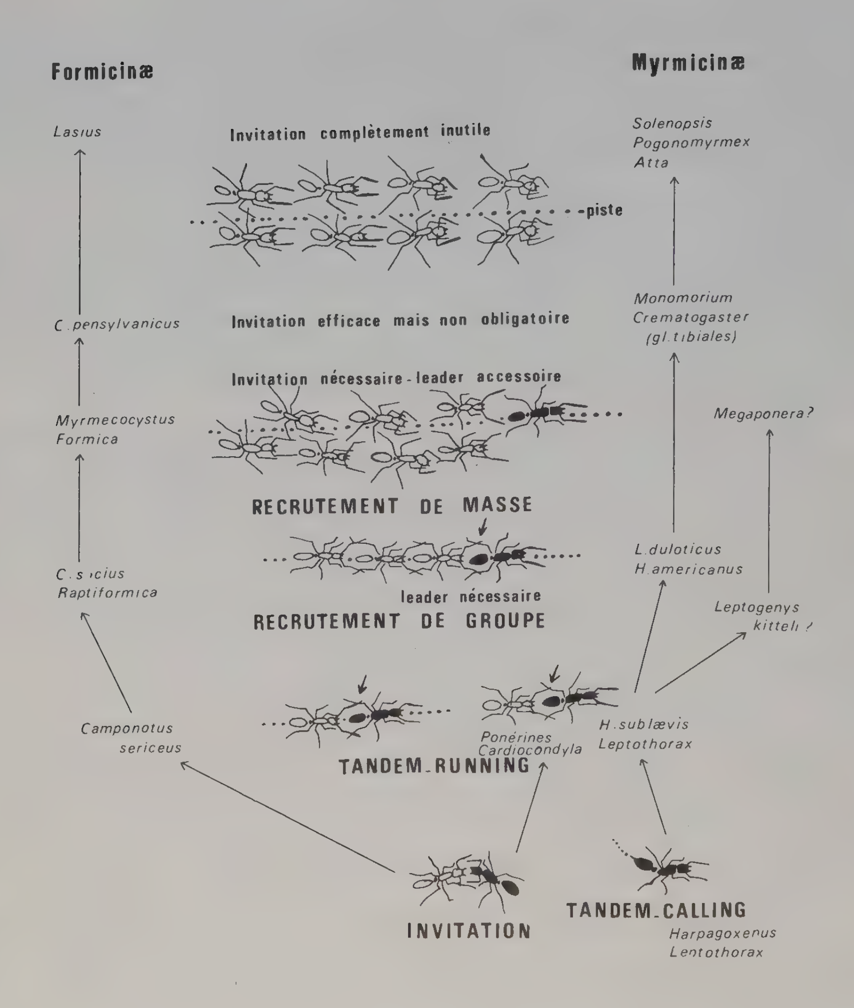


Fig. 1 — Schéma montrant l'évolution possible du comportement d'invitation chez les fourmis. Le comportement d'invitation existe chez toutes les fourmis sauf chez *Harpagoxenus* et *Leptothorax* où il est remplacé par le «tandem-calling». Chez les Formicines, les Myrmicines et les Ponérines, il peut être suivi de tandem-running, de sortie d'un groupe avec leader, ou d'un grand nombre de fourmis (recrutement de masse). Dans ce dernier cas le comportement d'invitation peut n'avoir qu'un rôle tout à fait secondaire et le signal chimique devient prépondérant. Pour chaque type on a noté quelques exemples.

Fig. 1 — Figure showing the possible evolution of the invitation behaviour in ants : invitation behaviour is present in all ant species except *Harpagoxenus* and *Leptothorax* were it is replaced by tandem-calling. In Formicinae, Myrmicinae and Ponerinae, it is followed by tandem-running, group or mass recruitment. In this last case invitation behaviour becomes secondary and the chemical signal is the most important. For each type we indicate some examples.

entier. On a reconnu les caractéristiques suivantes pour l'évolution de ce comportement.

Le comportement d'invitation est presque toujours associé au dépôt d'une trace. Le comportement d'invitation permet un recrutement à lui seul dans la sous-famille des Ponérines. Chez les Myrmicines, on connait deux exemples qui nécessiteraient d'être étudiés de manière plus approfondie où il ne semble pas exister de phéromone de piste : chez *Cardiocondyla* pour le tandem running ; et son existence est contestée chez *Pheidole pallidula* pour le recrutement de masse. Les travaux plus récents ont montré que son rôle était facultatif chez *Aphaenogaster.*

La règle générale de l'évolution semble être de permettre le recrutement d'un nombre plus grand de congénères en associant une trace au comportement d'invitation. On trouve tous les degrés depuis le recrutement purement tactile jusqu'à un recrutement purement chimique. Dans ce cas, le comportement d'invitation peut, soit disparaître au profit d'un nouveau comportement, le tandem calling, soit exister en tant que relique comportementale inefficace chez les espèces qui pratiquent le recrutement chimique de masse. Il pourrait exister dans certains cas intermédiaires comme le recrutement de groupe une phéromone d'invitation dont l'existence est à démontrer (Verhaeghe, 1977). Selon Hölldobler, 1977, p. 435) «le tandem calling» pourrait avoir évolué chez les Myrmicines vers la communication chimique de masse où les phéromones de trace sont émises par la glande à poison (règle générale chez les Myrmicines sauf pour les *Crematogaster*), mais il parait possible de penser aussi à deux évolutions divergentes, aboutissant l'une au tandem-calling sans invitation, et l'autre au recrutement de masse sans invitation.

Cette évolution peut se réaliser même à l'intérieur de certains genres. C'est le cas de *Camponotus* qui a été très étudié où l'on trouve des espèces à tandem-running primitif comme *C. sericeus* et d'autres à recrutement de masse comme *C. pennsylvanicus.* Il en est de même chez les Myrmicines avec *Harpagonexus sublaevis* et *H. canadensis* à tandem et *H. americanus* à recrutement de groupe.

A l'intérieur d'une même espèce on trouve des combinaisons de signaux pour des rôles de recrutement différents. Ainsi chez *C. socius* l'invitation pour une source de nourriture est une danse à frétillement latéral (waggle) associée à l'odeur de la nourriture offerte alors que l'invitation pour un déménagement est une danse à frétillement longitudinal (jerking). La phéromone de piste provient de l'intestin postérieur. On se rappellera aussi le cas des *Leptothorax* esclaves qui suivent les tandems ou les groupes lors de raids de l'hôte. Le cas le plus complexe semble réalisé chez *Oecophylla longinoda* qui utilise cinq systèmes de recrutement dont quatre comprennent des stimuli tactiles très

similaires : pour une source alimentaire l'invitation est de type «waggling», alors que pour l'émigration de la colonie, ou l'exploration d'un nouveau terrain ou le recrutement à longue distance contre les intrus, l'invitation est plutôt un «jerking». On a donc une situation comparable à celle de *C. socius*, la trace a pour origine une autre glande : la glande rectale. Le cinquième système de recrutement de *O. longinoda* est un recrutement à courte distance contre des intrus à l'aide d'une phéromone attractive émise par la glande sternale (Hölldobler et Wilson, 1978). Il semble que ce soit le répertoire le plus sophistiqué connu jusqu'à présent. *Il permet avec différentes combinaisons de signaux voisins d'assurer des fonctions variées.* Il semble que l'on retrouve ce phénomène chez *Myrmica*, où le comportement d'invitation paraît semblable lors du déménagement ou du recrutement alimentaire (Abraham et Pasteels, 1980). Les fourmis qui ne répondent pas au signal d'invitation sont transportées. La séquence est semblable au départ mais la transporteuse soulève fermement l'autre fourmi ce qui provoque le repli des pattes en position de nymphe de la transportée.

On notera que les termes de recrutement en tandem, groupe ou masse sont essentiellement descriptifs, mais ne renseignent pas sur l'*efficacité* du comportement. Verhaeghe et coll. (1980) ont abordé ce problème en terme de flux d'arrivée des ouvrières à la nourriture. Ils ont constaté que chez *Tetramorium caespitum* le rendement d'un recrutement de groupe est de 60 %. Il est à peine supérieur chez *Tapinoma erraticum* qui pratique un recrutement de masse : 73 %. Par contre, pour une ouvrière isolée remontant la piste, la probabilité de trouver la source de nourriture est très différente : 73 % chez *Tapinoma* et 10 % chez *Tetramorium*. Les espèces à recrutement de masse semblent bien adaptées pour exploiter des sources de nourriture importante. Chez les espèces à recrutement de groupe, le comportement moins déterministe des ouvrières le long de la piste permet la découverte de sources de nourriture nombreuses.

Le comportement d'invitation semble très spécifique des fourmis et peut-être des termites où il a été très peu étudié. Mais il n'a pas d'équivalent chez les abeilles et les guêpes, si l'on excepte le «backing and following» des *Lasioglossum*. Lorsqu'une abeille pourvoyeuse a découvert une source de nourriture, à son premier retour à la ruche, elle effectue une danse frétillante en courant, tout à fait semblable à celle que l'on observe chez les fourmis et les termites. Lors des voyages suivants, elle effectue la danse bien connue avec contacts antennaires entre les suiveuses et la danseuse (Schmid, 1964 in Wilson, 1971, p. 270). La danse pourrait donc être une forme ritualisée du comportement d'invitation. Chez les guêpes et les bourdons on connait très peu de choses : le recrutement se fait le plus souvent par l'odeur de la nourriture comme signal principal (Free, 1970 ; Maschwitz et coll., 1974).

Chez les Trigones et Mélipones, le recrutement évolue selon les espèces avec des sons, des phéromones de la glande mandibulaire et des danses en zig-zag (Lindauer et Kerr, 1960 ; voir aussi la revue de Hölldobler, 1977, p. 442).

Le seul cas où l'on aurait pu mettre en évidence un *véritable transfert d'information* sur une direction par le comportement d'invitation est dans le travail de Zabelin (1979) : chez *Tapinoma simrothi* dans un labyrinthe en croix, quand la nourriture est transférée d'une branche à l'autre, le flux d'ouvrières se réoriente progressivement de la vieille trace à la nouvelle. La sélection de la nouvelle trace est facilitée par les contacts tactiles entre les insectes allant vers le labyrinthe et ceux qui en reviennent avec de la nourriture. Si la nourriture est placée dans les deux branches simultanément, dans la plupart des cas, les fourmis partant vont dans la branche d'où reviennent les pourvoyeuses avec lesquelles elles ont eu des contacts. C'est une expérience importante qui, si elle était confirmée, donnerait partiellement raison aux anthropomorphismes des auteurs du début du siècle !

LES COMMUNICATIONS ANTENNAIRES DURANT LES ÉCHANGES ALIMENTAIRES

Les mouvements d'antennes accompagnant les échanges de nourriture ont été observés par Huber en 1810 chez les fourmis. Il distinguait le comportement d'invitation du comportement de sollicitation alimentaire : la pourvoyeuse qui rentre au nid invite ses compagnes à sortir avec des battements antennaires saccadés, alors qu'une fourmi utilise ses antennes et ses pattes antérieures pour solliciter de la nourriture à une congénère. Janet (1895) a observé aussi les trophallaxies chez le frelon et distingué la donneuse de la receveuse. On analysera dans un premier paragraphe les échanges d'aliment régurgité entre adultes.

Les échanges de nourriture regurgitée (Trophallaxie stomodéale) : chez les fourmis il est facile de reconnaître à l'observation, la donneuse de la receveuse. La première a, en général, l'abdomen gonflé par le miel emmagasiné dans son jabot ; elle le régurgite en laissant sourdre une gouttelette entre ses mandibules ouvertes. Ses antennes sont relativement immobiles, le plus souvent écartées, le scape dirigé vers l'arrière et le fouet parallèle à l'axe du corps. La receveuse au contraire palpe en permanence la donneuse à l'aide de ses antennes. Pour cela elle peut prendre appui sur la tête de sa partenaire avec ses pattes antérieures, tandis qu'elle se dresse sur ses pattes moyennes et postérieures. Le plus souvent sa tête est inclinée à 90° par rapport à celle de la donneuse.

Les séquences comportementales de la trophallaxie ont été décrites chez les fourmis par Wallis, 1961 (*F. fusca* et *F. sanguinea*), Hölldobler, 1970, 1973b (*F. sanguinea*), Lenoir, 1973a et b, 1979 (*M. laevinodis*), Torossian, 1972, 1973a et b (*Dolichoderus quadripunctatus*) ; chez les guêpes par Free (1956) et Montagner (1966), et chez les abeilles par Montagner et Pain (1971a et b, 1973). On rappellera que l'idée classique de la transmission de la substance royale de la reine d'abeille par trophallaxie n'est pas vérifiée (Seeley, 1979).

Free (1956) a décrit en détail les séquences comportementales de la trophallaxie chez l'abeille. La solliciteuse essaie d'introduire son proboscis entre les mandibules de la donneuse. Une abeille qui offre déploie son proboscis replié, de haut en bas et sur les côtés en direction de ses congénères, souvent en présentant une goutte de liquide régurgité entre ses mandibules. Les deux activités sont accompagnées de battements antennaires. Une tête d'abeille fraîchement coupée suffit à provoquer les comportements d'offre et de sollicitation. Les têtes sans antennes sont moins efficaces, les antennes servent donc de point de repère. L'odeur est importante : un tampon de coton peut suffire à provoquer les réponses s'il est imprégné de l'odeur de la tête. Les antennes servent donc à la fois pour localiser et solliciter la partenaire.

Montagner (1966) a repris sans succès, chez les guêpes, les expériences de Free avec la même technique : la tête n'est pas suffisante même avec des antennes animées de mouvements vibratoires. Il faut des signaux réciproques et une position subordonnée de la donneuse. L'étude fine des séquences comportementales chez les guêpes et les abeilles a montré qu'il existe 3 types de rituels antennaires durant la trophallaxie stomodéale (Montagner, 1966 ; Montagner et Pain 1971a et b, 1973).

– La receveuse stimule la donneuse. Cette stimulation sert à déclencher la régurgitation de l'ouvrière sollicitée et à maintenir avec elle un contact durable. Elle se réalise par un balayage transversal des mandibules et de l'espace intermandibulaire de la donneuse.

– Le 2ème type de rituel est la conséquence de la stimulation de la donneuse par la receveuse. Chez les guêpes la donneuse rabat son antenne active au niveau des mandibules de la solliciteuse qui, à son tour, réagit en repoussant l'antenne de la donneuse. Il y a ainsi une phase très rapide de compétition entre les deux funicules des deux partenaires, qui se termine par le retrait de l'antenne active de la donneuse et par un prolongement de la régurgitation. Ce rituel est un peu plus compliqué chez les abeilles où l'une des antennes de la donneuse stimule très souvent le proboscis de la solliciteuse, ce qui est interprété comme un signal d'acceptation, car la solliciteuse ne cherche pas à repousser cette antenne.

Chez les fourmis. Wallis (1961) n'a pas réussi à reconnaître des signaux précis pendant les échanges. Hölldobler (1973) a montré à l'aide de films que, chez *F. sanguinea*, la solliciteuse s'approche d'une congénère et la stimule au niveau des pièces buccales (labium) par ses antennes et ses pattes antérieures, ce qui déclenche la régurgitation. Il est possible de déclencher la régurgitation de fourmis gavées en stimulant artificiellement leur labium. La donneuse peut élever ses pattes antérieures et effectuer ses propres mouvements de sollicitation, en particulier pour rompre l'échange. L'intervention des pattes antérieures dans la trophallaxie est une caractéristique des fourmis. On a montré que chez *Myrmica* les pattes n'interviennent durant l'échange que dans des circonstances bien précises, par exemple pour changer de position ou pour répondre à une stimulation de la donneuse. La fin de l'échange est précédée de battements des tarses qui servent ensuite de point d'appui pour le retrait de la receveuse (Lenoir, 1973a). Chez *Lasius*, la receveuse utilise ses pattes antérieures tout au long de l'échange de nourriture. Elle effectue des palpations plus ou moins rapides selon son niveau de motivation. On se rapproche des comportements décrits par Wallis pour les *Formica*. Le rôle des pattes antérieures est beaucoup plus important chez les Formicines que chez les Myrmicines dans le déroulement de la trophallaxie (Lenoir, 1973b).

LES SÉQUENCES ANTENNAIRES DES FOURMIS (Fig. 2)

Les séquences antennaires des fourmis ont été étudiées chez *Myrmica* (Lenoir, 1973a). On retrouve les 2 types de réactions caractéristiques de la sollicitation et de l'acceptation. La compétition antennaire se présente d'une manière particulière puisque c'est l'extrémité du funicule de la receveuse qui vient frapper la base du scape de la donneuse. La compétition entre les 2 funicules existe, mais elle s'observe rarement. Les zones antennaires mises en jeu sont donc différentes selon les groupes. On a montré que la topographie sensorielle de l'antenne est adaptée à cette forme de stimulation et de communication (Lenoir et Jaisson, 1974).

Ainsi les échanges trophallactiques des fourmis s'accompagnent de mouvements antennaires à valeur informative, qui semblent s'apparenter au type décrit chez l'abeille. On trouve en effet les mêmes différences entre abeilles et guêpes qu'entre fourmis et guêpes :

– Il n'y a pas de contrôle permanent des substances régurgitées.

– Il n'y a pas non plus de postures en relation avec un rang social de l'individu qui serait lié à la trophallaxie. Torossian signale aussi l'absence de hiérarchie pour l'aliment proctodéal (1973b). Les différences avec les abeilles n'en sont pas moins grandes :

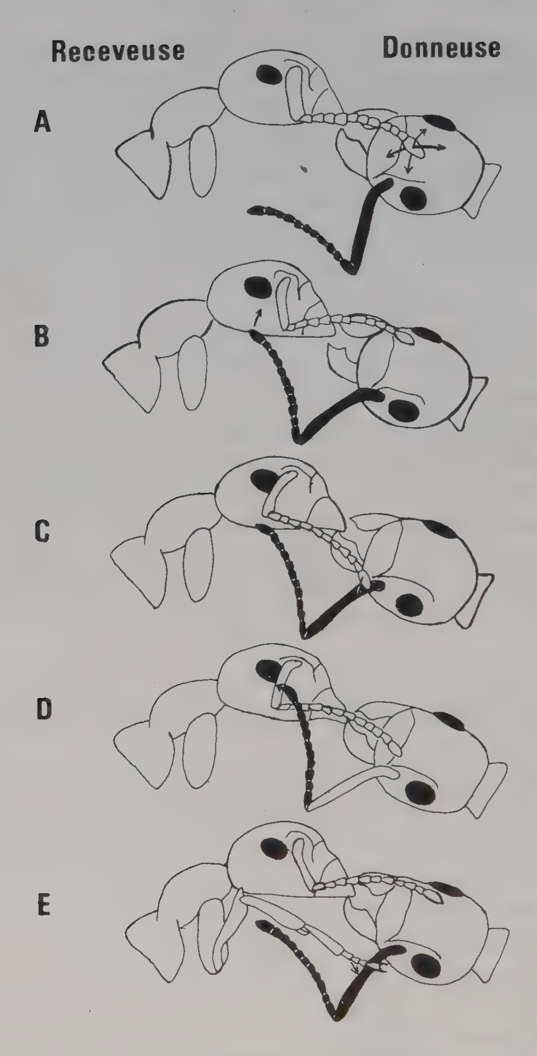


Fig. 2 – Contacts antennaires durant la trophallaxie chez *Myrmica* : receveuse à gauche de profil, donneuse à droite – A : palpations de la receveuse sur la tête de la donneuse – B : palpations de la donneuse sur la tête de la receveuse – C : réactions de la receveuse au contact antennaire de la donneuse ; la receveuse repousse la base de l'antenne active de la donneuse – D : parfois la donneuse agit de même, on a ainsi des périodes de compétition interantennaire – E : fin de la trophallaxie : la receveuse se retire en repoussant l'antenne active de la donneuse avec sa patte antérieure.

Fig. 2 – Antennal contacts during trophallaxy in *Myrmica* : receiver on left, donor on right – A : palpations of the receiver on the head of the donor – B : palpations of the donor on the head of the receiver – C : reactions of the receiver to antennal contact of the donor : the receiver pushes the base of the active antenna of the donor – D : sometimes the donor have the same movement, we have periods of interantennal competition – E : end of the trophallaxy : the receiver withdraws by pushing the antenna of the donor with its foreleg.

– le signal d'acceptation n'est pas le même chez les fourmis,

– la compétition interantennaire ne se déroule pas de la même manière,

– Enfin, et c'est peut-être ce qui frappe le plus, les réactions des deux partenaires paraissent peu liées. Il est difficile de prévoir le comportement d'une fourmi à l'observation de sa partenaire. Au premier abord les battements sont de simples caresses transversales plus ou moins rapides. Pour cette raison nous avons essayé d'approfondir l'analyse de ce système en recourant à la théorie de l'information (voir, par exemple, la revue de Losey, 1978).

On a montré (Lenoir, 1982) que la quantité d'information transmise entre 2 fourmis par les contacts antennaires correspond à peine à 10 - 20 % de la quantité du message émis (transmission normalisée). Les comportements de la donneuse et de la receveuse ne sont liés quantitativement que pour une faible part[1]. Cela permet de comprendre certains auteurs comme Masson (1974) qui, décrivant les structures proprioceptives et tactiles de l'antenne de *Camponotus*, pensent que l'existence de signaux ritualisés n'est pas prouvée chez les fourmis. S'ils existent, ils sont noyés dans une masse de mouvements antennaires et tarsiens. Ceci n'exclut d'ailleurs pas la possibilité que les rituels aient une importance fondamentale dans le déroulement de la trophallaxie. C'est un problème à aborder sous l'angle électrophysiologique. La quantité d'information transmise par la danse des abeilles ou les traces de *Solenopsis* est beaucoup plus importante et peut atteindre 70 % (Wilson, 1962). Il y a indication de distance et de direction, alors que les partenaires d'une trophallaxie n'ont besoin de renseignements que sur leur état de motivation réciproque. Les communications antennaires semblent se rattacher au système de *communication par modulation* tel qu'il a été décrit pour les vibrations (Fuchs, 1976 ; Markl et Hölldobler, 1978). C'est une forme de communication qui permet l'élévation du niveau d'activité du partenaire. On peut ainsi comprendre l'existence de trophallaxies sans aucun mouvement d'antennes comme cela se produit parfois chez *Camponotus* (Lenoir, 1973a).

Les colonies mixtes permettent aussi d'aborder ce problème. Jaisson (1969) a montré que les *Aphaenogaster* qui ne pratiquent pas la trophallaxie, élevées avec des *Myrmica*, peuvent être receveuses dans des échanges interspécifiques et employer des mouvements antennaires qui semblent très proches de ceux des *Myrmica*. Plus récemment il a réalisé des colonies mixtes avec de nombreuses espèces de Formicines, et observé des trophallaxies entre *Camponotus vagus* de grande taille et *Camponotus merula* de toute petite taille. Les antennes de la grande *C. vagus* receveuse sont beaucoup plus longues

1 – Les données récentes de Bonavita (à paraître) sur les communications antennaires pendant la trophallaxie chez *Camponotus vagus* confirment qu'il est impossible de mettre en corrélation des rituels antennaires avec les réactions de la partenaire. Il apparaît que «l'ouvrière donneuse régurgite à la condition d'être stimulée activement dans la région mandibulaire... avec des balayages rapides, par contre les actes de la donneuse ne constituent pas des signaux pour la receveuse».

que le corps de la petite *C. merula* donneuse. Cela montre l'aspect facultatif des contacts antennaires chez les fourmis (Jaisson, 1980). Cet aspect facultatif est montré aussi par des *sections d'antennes* : en général les possibilités des individus dépendent du nombre d'articles antennaires enlevés (Jaisson, 1969). Il en est de même chez les abeilles antennectomisées qui peuvent offrir mais sont incapables de solliciter (Free, 1956). Galliot et Azoeuf (1979), avec des isotopes radioactifs, montrent que la section des deux articles distaux des antennes n'a pas de conséquences sensibles, alors que l'amputation des 4 derniers articles entraîne une chute de 75 à 80 % de l'activité trophallactique des opérées. Elle pourrait résulter à la fois d'une perte des sensilles, d'une perte d'efficacité dans la stimulation des mécanorécepteurs des donneuses, et d'une augmentation des comportements d'agression.

Les pseudotrophallaxies des Ponérines (ce terme a été créé par Jaisson et Fresneau, 1978) : chez *Neoponera* une pourvoyeuse peut rapporter une goutte de miel entre ses mandibules et être sollicitée par des congénères qui viennent sucer le liquide. Pendant la durée de l'échange on observe des contacts antennaires entre les 2 fourmis, avec des interactions apparemment proches de celles que l'on peut observer durant une véritable trophallaxie chez d'autres espèces, mais l'analyse fine des mouvements reste à faire. Young (1977) a observé des pourvoyeuses de *Paraponera* transportant une gouttelette de sève entre leurs mandibules. Il est vraisemblable qu'il s'agit du même comportement et que la goutte est partagée dans le nid. Cela pourrait être une caractéristique d'évolution secondaire chez les fourmis qui ne pratiquent pas la trophallaxie. C'est-à-dire que la pseudotrophallaxie serait un comportement de substitution, analogue à la trophallaxie dans sa fonction. L'importance quantitative des pseudotrophallaxies dans le flux de nourriture de la colonie reste à apprécier. C'est ainsi que Fellers et coll. (1976) ont décrit chez *Aphaenogaster* un transport d'eau à l'aide de graviers ou de feuilles. Les espèces qui ne peuvent transporter des liquides dans leur jabot ont «inventé» d'autres systèmes leur permettant un transport et la distribution s'effectue avec les mêmes schèmes antennaires que dans la trophallaxie.

Trophallaxies avec les myrmécophiles : les myrmécophiles peuvent solliciter avec leurs antennes et leurs pattes antérieures exactement à la manière d'une fourmi (stimuli tactiles) et obtenir une trophallaxie mixte. C'est le cas d'*Atemeles* et *Lomechusa* dans le nid de *Myrmica* ou de *Formica* ; d'*Amphotis* le long des pistes de *Lasius fuliginosus* (Hölldobler, 1970, 1973). Les *Dinarda* dérobent occasionnellement une goutte de liquide pendant un échange. Ils peuvent aussi s'approcher d'une pourvoyeuse gavée et par stimulation des pièces buccales obtenir une régurgitation, mais la fourmi réagit en attaquant le coléoptère qui s'enfuit (Hölldobler, 1973). Ainsi des myrmécophiles savent copier les signaux tactiles utilisés par les fourmis, cela est

possible parce qu'il n'y a pas de signal spécifique chez les fourmis. La meilleure adaptation est celle qui utilise aussi la reconnaissance chimique et permet des trophallaxies complètes. Les *Claviger* étudiés par Cammaerts (1977) représentent un cas tout à fait original. Il semble qu'ils sont perçus comme des cadavres. La fourmi-hôte (*Lasius flavus*) régurgite de la nourriture sur les cadavres (les sécrétions de *Claviger* pourraient ressembler aux substances de putréfaction des cadavres). C'est le seul cas connu de déclencheur chimique de la régurgitation, les mouvements antennaires des *Claviger* sont inefficaces.

Les trophallaxies abdominales : sont des échanges alimentaires dans lesquels un individu solliciteur se nourrit avec du liquide provenant de l'abdomen du partenaire. Si le liquide a pour origine le rectum on parlera de trophallaxie proctodéale, sinon on emploie le terme plus vague de trophallaxie abdominale. Les véritables trophallaxies proctodéales ne semblent exister que chez les Termites mais on ne connait pas, avec précision, les séquences comportementales qui les accompagnent. Les trophallaxies abdominales sont les plus importantes chez *Dolichoderus quadripunctatus*, étudiées par Torossian (1973a, b) à l'aide de films. Les échanges sont précédés d'une phase de sollicitation en face à face, plus ou moins longue selon l'état saisonnier de la colonie, avec deux types de séquences qui alternent : des contacts antennaires rapides, et des caresses céphaliques lentes. La réponse de la donneuse se traduit par l'émission par le cloaque d'une gouttelette alimentaire (œuf trophique) qui est aussitôt absorbée par l'ouvrière solliciteuse. Les ouvrières de *Myrmecia gulosa* pratiquent une sollicitation de même type pour obtenir un œuf trophique (Freeland, 1958). Wilson (1976) décrit chez *Zacryptocerus varians* une trophallaxie abdominale avec sollicitation antennaire de l'abdomen qui est semblable à une sollicitation pour obtenir une régurgitation et qui aboutit à l'émission d'une gouttelette dont l'origine est inconnue. Ce comportement n'existe pas chez les autres *Cephalotini* et semble unique chez les fourmis.

Les trophallaxies avec les larves. Les ouvrières nourrissent les larves avec du liquide régurgité. Chez *Lasius* (Lenoir, 1979) il n'existe pas de position privilégiée de l'ouvrière par rapport à la larve : les petites larves sont parfois saisies avec les pattes antérieures, et l'ouvrière place la tête de la larve directement au contact de sa bouche, le plus souvent à 180°. La régurgitation s'accompagne de mouvements antennaires dirigés vers la larve. Les ouvrières peuvent solliciter les larves et obtenir ainsi une gouttelette de sécrétion buccale ou anale. Chez les fourmis on peut citer la revue de Le Masne (1953). C'est un comportement très fréquent chez les guêpes où les sécrétions larvaires jouent un rôle important dans le flux trophique et il est facile de déclencher la sécrétion de salive des larves avec un pinceau. Il s'agit donc de stimuli tactiles très peu spécifiques (Montagner, 1966 ; Maschwitz, 1966, Ishay et Ikan, 1968).

En conclusion, comme pour le comportement d'invitation on a dans la trophallaxie des *signaux tactiles* très généralement répandus, mais qui semblent avoir peu évolué :

– aux battements antennaires viennent s'ajouter le plus souvent, chez les individus très motivés, des mouvements de pattes antérieures qui ont une importance indéniable au moins chez les Formicines ;

– les mouvements d'antennes et de pattes ont un rôle essentiellement *mécanique* de stimulation de la tête et des pièces buccales de la donneuse sollicitée, puis des contacts réciproques qui permettent l'entretien de la trophallaxie. Les signaux deviennent facultatifs chez les fourmis où l'on peut observer des échanges sans mouvements antennaires, ou des échanges mixtes sans contacts avec les antennes. C'est un système de communication de modulation. On retrouve les mêmes schèmes moteurs dans la sollicitation abdominale, ou dans la sollicitation des larves, ou encore dans la traite des pucerons ;

– chez les guêpes on trouve des rituels bien développés en relation avec l'échelle sociale des individus. Ces rituels n'existent pas dans les autres groupes où l'on ne peut reconnaître une hiérarchie ;

– si le comportement d'invitation est associé le plus souvent à des phéromones ce n'est pas le cas de la trophallaxie. L'odeur de la nourriture est le seul signal utilisé. On connait un seul exemple de déclencheur chimique de la régurgitation, c'est l'odeur des cadavres chez *Lasius flavus*, odeur mimée par les *Claviger*.

CONCLUSION GÉNÉRALE

Il semble donc que les communications antennaires aient évolué à partir de schèmes moteurs simples existant dans tous les groupes : des battements dirigés sur le partenaire avec balayage transversal ou longitudinal. On reconnait deux lignes principales dans l'évolution :

– Association avec des signaux chimiques dans l'invitation et l'importance de plus en plus grande des phéromones. Dans les cas les plus évolués, le comportement d'invitation subsiste à l'état de relique. Le message chimique individuel émis par les pourvoyeuses revenant au nid dépend de la privation de nourriture, de la qualité et de la distance de la source de nourriture et permet ainsi une grande flexibilité dans la communication de masse (Hangartner, 1969 ; Jaffé et Howse, 1979).

– Association avec les mouvements des pattes antérieures pour augmenter le rôle mécanique dans la stimulation du partenaire. La stimulation

antennaire est utilisée à d'autres fins par exemple dans la traite des pucerons, ou la sollicitation des larves, elle est mimée par des myrmécophiles.

Le rôle tactile des antennes est obligatoire et ritualisé, lié à une échelle sociale et à une compétition chez les guêpes, il devient, au contraire, facultatif au moins en partie chez les fourmis. Les communications antennaires ne semblent pas témoigner d'un niveau phylogénétique dans l'organisation des insectes sociaux. Tout au plus peut-on signaler une variété plus grande dans le comportement d'invitation chez les Formicines, mais il faudrait analyser les séquences de manière très précise pour conclure.

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THE BIOLOGY AND BEHAVIOUR OF
THE HONEYBEE *APIS FLOREA*

J.B. FREE

Rothamsted Experimental Station,
Harpenden, Hertfordshire, England

SUMMARY

Our present knowledge of various aspects of the behaviour and biology of *Apis florea* (including temperature regulation, foraging, communication, colony reproduction, absconding and migration) is reviewed and suggestions made for further studies. Present methods of beekeeping with *Apis florea* colonies are described, and developments that are necessary to improve beekeeping are discussed.

RESUMEN

La Biologia y el comportamiento de la abeja Apis florea

Nuestros conocimientos actuales sobre varios aspectos del comportamiento y biología de *Apis florea* (incluyendo regulación de temperatura, forageo, comunicación, reproduccion de la colonia, huida y migracion) son revisados y se presentan sugestiones para estudios posteriores. Los métodos actuales de cria con las colonias de *Apis florea* son descritos, y los desarrollos que son necesarios para incrementar la cría son discutidos.

Apis florea is one of the four species of honeybee of the genus *Apis*. Although it is among our most advanced social insects, knowledge of it is fragmentary and most is assumed by implication from discoveries about *Apis mellifera*. I will briefly review existing knowledge and indicate research

topics that are potentially rewarding. *Apis mellifera* occurs from Oman and Iran in the West, through the Indian sub-continent to Indonesia in the East. It is absent north of the Himalayan mountains (Stitz & Szebe, 1903, Buttel-Reepen, 1906, Maa, 1953).

Nest and comb

An *Apis florea* colony usually builds a single wax comb, up to 35 cm wide and 25 cm deep, which is often attached to the thin branch of a bush or tree. The upper part of the comb forms a «crest» above and surrounding the supporting branch and is used for storing honey ; cells of the crest may be two or three times the length of those below. The top of the crest forms a wide approximately horizontal platform. Below the crest is the area for storing pollen and rearing brood, the pollen occurring as a band between the honey and brood. Most of cells below the crest are workers, but in mature colonies a band of drone cells are built along the lower edge of the comb, and drone brood may occupy between a quarter and a third of the total brood area (Thakar & Tonapi, 1962 ; Sakagami & Yoshikama, 1973). Drones are relatively large compared to other *Apis* species. The size of the worker cells and the adult workers increases from South to North (Rahman & Singh, 1946). But no attempts seem to have been made to investigate the relative importance of environmental and inheritance in determining this trend.

Worker activities

The comb of an *A. florea* colony is enveloped by a curtain of workers, three or more bees thick, that protect the colony from enemies and from extremes of heat and cold. Bees regulate the temperature of their brood nest within fairly narrow limits ; at environmental temperatures ranging from 18 to 33°, the bees maintained the central area of the comb between 33 and 37° (Lindauer, 1957 ; Akratanakal, 1977 ; Free & Williams, 1979). It is agreed that with increase in environmental temperature the distance between the curtain of bees and the comb increases, but there is a discrepancy as to whether the bees become more or less tightly packed under such circumstances. Although it is known that bees collect water it is not certain whether they use it to cool their colony. Ventilation fanning occurs but bees fan only when in direct sunlight and by merely shading the comb they can be made to cease fanning immediately (Free & Williams, 1979).

Apis florea colonies need to defend themselves against a variety of enemies including ants, hornets, other *Apis* species and man (Koeniger &

Fuchs, 1975 ; Akratanakal, 1977). When an intruder does land on the comb it is attacked by defending *A. florea* workers which are sometimes so numerous that they form a clump around it. Such a clump of bees often passes slowly down the curtain of bees covering the comb, forms a bulge at the comb base, and eventually drops off onto the ground (Free & Williams, 1979). The degree of aggressiveness shown by *A. florea* varies greatly (Ghatge, 1949 ; Morse et al., 1967 ; Akratanakal, 1977). In Oman attempts to induce *A. florea* to fly to the attack were unsucessful. The curtain that helps protect the colony obscures the activities of bees on the comb surface, and makes it difficult to study the colony's social organisation. It has been estimated that up to 80 % of the adult workers are in the curtain (Akratanakal, 1977) ; if so this seems to be a relatively ineffective way of using the labour force, even if bees in the curtain do perhaps spend some time secreting wax and brood food.

Nothing is known about the division of labour among the workers. Much could be learned by marking, observing and dissecting individuals. Sandwiching the part of the comb that is beneath the crest between sheets of glass, so the curtain is reduced to one bee thickness, should facilitate observation. Most foragers visit the crest platform on return to their nest. The pollen gatherers then proceed to the comb face, but many nectar gatherers remain on the crest or supporting stick throughout the time they are in the nest and give nectar to the other bees (Free & Williams, 1979). Foragers also indicate a food source by round dances and wagtail dances on the crest platform, the straight run of the wagtail dance pointing directly to the food source (Lindauer, 1957). It was believed that the comb of *A. florea* is always built round a branch, where the bees have a good view of the sky, and that when dancing bees were unable to see the sky their dances were disorientated. It was also supposed that *A. florea* is only capable of the direct form of communication possible in a horizontal dance, and is unable to transform information to a vertical plane (Lindauer, 1957).

However, it is now known *A. florea* colonies frequently suspend their comb from cave rooves, where sky is not always visible from the comb and there is no horizontal platform (Dutton & Simpson, 1977 ; Dutton & Free, 1979). In these circumstances bees dance on the vertical comb surface. Resting a sheet of cardboard on top of the crest platform so bees were unable to dance on it, induces foragers to perform vertical dances on the upper surfaces of the comb face (Lindauer, 1957 ; Free & Williams, 1979).

Investigations are need to determine :

– whether dances on the vertical comb face are correctly orientated,
– whether a dancing bee needs to be able to see the sky,
– the distance to the source of forage at which round dances are superceded by wagtail dances.

Studies on the location and direction indicating efficiency of dances made by bees in the swarm should also prove rewarding.

There are a number of behaviour patterns whose function is unknown (Free & Williams, 1979). For example, bees scattered over the surface of the curtain hold their wings slightly extended, raise their abdomens and move them vigorously from side to side. Often each performing bee has a circle of others facing toward her. After a few seconds she moves on and performs elsewhere. This dance is performed before a colony absconds ; perhaps it occurs in other circumstances also.

Reproduction

Near the peak of colony growth swarm queen cells are produced along the edge of the comb (Ghatge, 1949 ; Thakar & Topani, 1962 ; Tirgari et al., 1971). Little is known about the swarming process although it appears that the old queen leaves with the first swarm. A colony may continue to send off up to five swarms headed by virgin queens, until few or no bees remain in the parental nest (Akratanakal, 1977). Contrary to previous suppositions it has been shown that on removal of the queen, emergency queen cells are produced by modifying worker cells containing eggs and young larvae (Free & Williams, 1979). Once emergency queen production has begun it may continue even after a colony's queen has been returned. Preliminary tests have been made of the response of *A. florea* workers to cages, containing queen odours, presented at the periphery of the comb. Workers were attracted to their queen, and to the odour alone of their queen and many exposed their Nasonov glands ; they were similarly attracted to the odour of 9-oxo-*trans*-2-decenoic acid (9-o-2, the major component of the queen's mandibular glands) but without Nasonov gland exposure.

A stationary queen on the comb is surrounded by a «court» of workers. When polyethylene blocks were impregnated with 9o2 and put on the comb surface they were surrounded by a circle of workers that looked similar to the court surrounding a stationary queen. However, 9-hydroxy-trans-2-decenoic acid (9H2) another major component of the mandibular gland pheromone failed to elicit such a response, either alone or with 9o2. (The additions of 9H2 also diminishes the attractiveness of 9o2 to *A. mellifera* workers). These experiments obviously need expanding, and the effect of 9o2 compared with the extract of the queen's mandibular glands and other odours.

Colony absconding and migration

A colony may abscond two or three times a year. There seem to be three main causes : scarcity of forage ; high temperatures ; attacks by predators

(Pandley, 1974). Scarcity of forage is probably the main factor concerned and could be the primary one responsible for the supposed seasonal migration from the plains to the hills where forage is more abundant. However, proof of such long distance migration is lacking. Temperature changes are also important in governing changes of nest site, often within a small area (Tirgari, 1971 ; Koeniger, 1976 ; Dutton & Free, 1979). At the beginning of the hot season colonies move into the dense foliage of trees and bushes and move back from the entrances of caves for protection from the sun ; at the approach of cooler conditions colonies move forward in the caves and to the south side of trees and bushes where the early morning sun strikes the comb. Both accurate communication of the nest site and integral colony movement must be involved in migration but these have been little studied.

Foraging

It is well known that *A. mellifera* foragers collecting sugar syrup release a pheromone from their Nasonov glands that attracts recruits. In contrast, *Apis florea* does not expose its Nasovov gland when visiting rich sources of forage, but, the bees do leave a pheromone at the source of forage that is attractive to other foragers (Free & Williams, 1979). *A. mellifera* foragers use a similar forage-marking pheromone (Ferguson & Free, 1979) ; it is probably a more primitive form of communication than the Nasonov pheromone.

A. florea honey is highly esteemed for its quality and reputed medicinal and mystical properties (Drieberg, 1922 ; Muttoo, 1956), and in many countries the combs are collected for human consumption (Beeson, 1941 ; Morse & Benton, 1967 ; Sakagami & Yoshikawa, 1973 ; Akratanakal, 1977 ; Dutton & Free, 1979). Although brood is often eaten as well honey, sometimes the honey-gatherers remove only the crest of the comb for consumption. The remainder of the comb is sandwiched between the split stalk of a date palm leaf, the ends of which are suspended from the branches of a tree or rested on supporting stones. In time, bees build a new crest over the date palm stalk and more cells are built in the lower part of the comb to house the brood. When the new storage cells are in turn filled with honey, the beekeeper cuts them away again. Such a method of beekeeping has two main problems associated with it :

Firstly, present methods of taking the honey crop wastes wax comb, and necessitates much wax production and reconstruction by the bees. However, when the honey storage section of a comb is put on in a wooden frame, immediately above the brood section, the workers rapidly spread over the two adjacent frame bars. Possibly therefore, a system of beekeeping could

be devised in which the honey storage section of the comb be removed in its frame and returned to the colony after the honey had been extracted.

Secondly, the tendency of colonies to abscond must be discouraged. A possible way might be to confine the colony in a box or hive whose entrance is covered with appropriate queen excluder gauze, so the workers can forage but the queen is confined to the hive. Clearly, there is much scope for improvement in beekeeping techniques. Hopefully future investigations into colony organisation and behaviour will provide the answers.

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PLANTS WHICH SUPPLY «HAIR» MATERIAL FOR NEST BUILDING OF *PROTOPOLYBIA SEDULA* (SAUSSURE, 1854)

V.L. LETIZIO MACHADO

Departamento de Zoologia, Instituto de Biociencias
Campus de Rio Claro – S.P. Universidade Estadual Paulista
«Julio de Mesquita Filho» Brazil

SUMMARY

This wasp builds nests with lignified plant-hairs of different types. They are usually mixed with saliva and applied to the nest in a few layers, showing different colours in accordance with the source of the material. Sources were plants as different as Compositae of the cerrado, Menispermaceae (*Cissampelos ovalifolia*), Labiatae (*Leonotis nepetaefolia*), Loganiaceae (*Budleya brasiliensis*), Meliaceae (*Melia azedarach*). The nest building is usually correlated with the swarming.

RESUMEN

Los «pelos» de plantas utilizados para la construccion del nido en P. sedula

Las evidencias muestran que las avispas construyen sus nidos con pelos de plantas lignificados de diferentes tipos. Estos pelos son comunamente mezclados con saliva y depositados en pocas capas sobre el nido, en colores que varian con la naturaleza y origen del material empleado. Fueron reconocidos en este estudio, pelos de diferentes plantas como las Compositae del «Cerrado», Menispermaceae (*Cissampelos ovalifolia*), Labiatae (*Leonotis nepetaefolia*), Loganiaceae (*Budleya brasiliensis*) y Meliaceae (*Melia azedarach*). La construcción de los nidos es a menudo correlacionada con la enjambrazón.

INTRODUCTION

The nests of social wasps are usually made with vegetable materials worked up into a sort of paper. The raw vegetable material used to build nests consists mostly of wood fibers (as in the genus *Polistes, Polybia*, etc.), cotton (*Dolichovespula saxonica*), plant-hairs (*Apoica, Protopolybia*), and mud in some species of Polybiinae (*Polybia emaciata, P. singularis* and *P. spinifex*) : Möebius, 1856 ; Richards, 1951 ; Naumann, 1970. Social wasps shown some basic types of nests, characteristics of the species. However, the extent to which the nest material of each species of wasps is related to a given kind of plant supply is not known. The present study was undertaken in an attempt to determine the sort of material used by *Polybia sedula* to build up their nests as well as the sources of such material.

MATERIALS AND METHODS

The nests of *P. sedula* used in this study were collected around Rio Claro (22°25' S ; 47°33' WGr.), state of São Paulo, Brazil. Only the carton envelope was used to avoid contamination by alien objects and waste materials which could be present in combs and interfere the chemical analysis. The fine structure of the carton envelope was observed with the light microscope. For chemical analysis the carton envelopes were finely ground and treated by Kjeldahl's method to determine protein content by percentage, Munsen and Walker method to quantify total and reductors sugars ; cellulose and hemicellulose content were assessed by fibers methods. Direct observations in the foraging area were carried out to trace the main sources of the raw material used by the wasps to make the cartons.

RESULTS AND DISCUSSION

All the nests of *P. sedula* analysed were built with plant-hairs of different shapes, mixed with secretions probably from salivary glands, and arranged in thin and weak layers of carton. The specific stain for cellulose (blue solution) and lignin (phloroglucinol) showed that the material used was not cellulosic but lignified plant-hairs. This basic raw material was found in the whole nest sample studied but different kind of them were used according to the plants species available in the foraging area. It was clear that for each nest there was a predominance of a given shaped plant-hair. However, many kinds of plant-hairs were occasionaly used as well as digested cells, pollen grains, raphides, etc. Some nests, transferred far from the original foraging area, showed different plant-hairs which gave a distinctive color to the new

carton. This shows the opportunistic choice of raw material in this species. The small size of *P. sedula* made it difficult to track the wasps. Therefore the plants visited by the foragers were observed in order to determine the kinds of plant-hairs which the wasps used. In the sample studied the T-shaped plant-hairs (fig. 1) came from some species of Compositae from the «cerrado», the tufted hairs (fig. 2b and 3) from many plants such as *Cissampelos ovafolia* (Menispermaceae), «Cordao de Frade» *Leonotis nepetaefolia* (Labiatae), «Budleia» *Budleya brasiliensis* (Loganiaceae) and unidentified Tiliaceae. The simple plant-hairs were collected from «Guava» *Psidium guayava* (Myrtaceae) (fig. 2a), and the stellate hairs (fig. 4) came from stems and leaf stalks of chinaberry or pride of India *Melia azedarach* (Meliaceae). The weakness of the nests in this species, a result of the kinds of material employed, seems to be related to the frequent swarming of this species which has a complete nest cycle of about 90-100 days, the shortest recorded among social wasps (Rodrigues, 1971).

Legend for encircled figures 1 to 4 : partial view of nests of *Protopolybia sedula's* showing the arrangement of the plant-hairs used to built the envelop, and detail of the hair predominant in each nest.

Leyenda en los círculos de las figuras 1 a 4 : vista parcial de los cartones de nidos de *Protopolybia sedula* mostrando la disposición de los pelos empeleados y detalle del pelo predominante en cada nido.

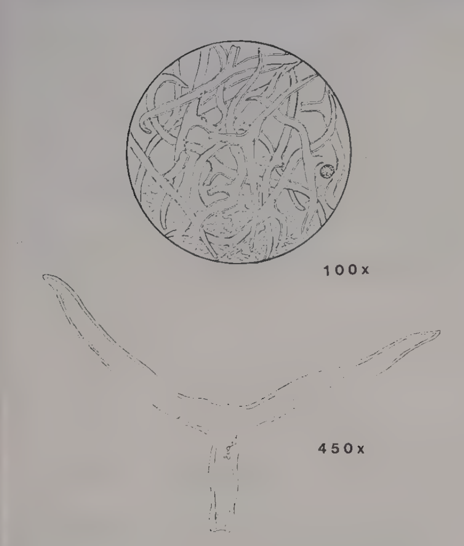


Fig. 1 – Lignified hair of a Compositae from «Cerrado»

Fig. 1 – Pelo lignificado de una Compositae del «Cerrado».

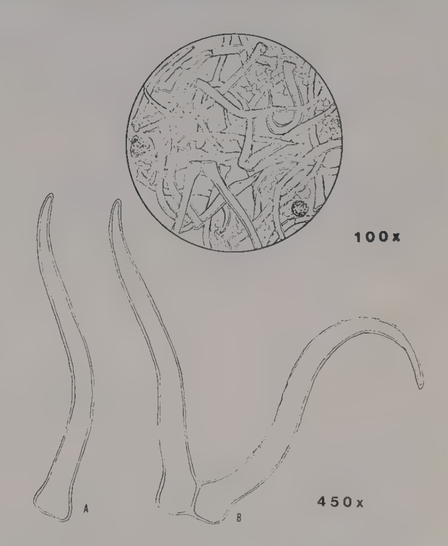


Fig. 2 – A : Simple hair of a Myrtaceae – B : Tufted hair from Menispermaceae, Labiatae, Loganiaceae et Tiliaceae.

Fig. 2 – A : Pelo simple de Myrtaceae – B : Pelo ramificado y lignificado provenientes de Menispermaceae, Labiatae, Loganiaceae y Tiliaceae.

Chemical analysis of the carton envelope reveled 8.6 % proteins ; 2.3 % total sugar, 1.3 % of which was reducing sugar ; 17.7 % of fibers (cellulose and hemicellulose) probably corresponding to the cellulose found in the membranes of digested cells, pollen, grains, etc. These chemical analysis gave an estimated composition of the nest material only as few samples were available per nest.

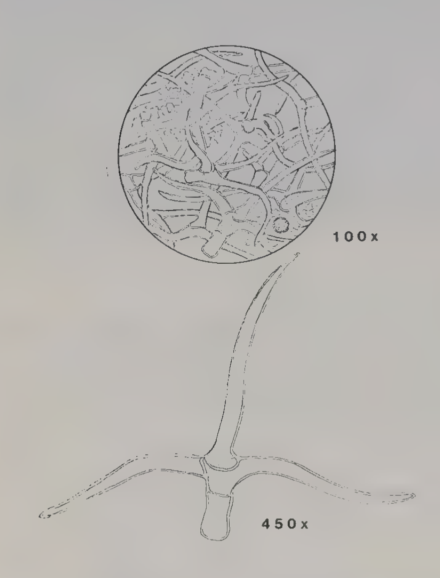


Fig. 3 – Tufted and lignified hair from Menispermaceae, Labiatae, Loganiaceae and Tiliaceae.

Fig. 3 – Pelo ramificado y lignificado proveniente de Menispermaceae, Labiatae, Loganiaceae y Tiliaceae.

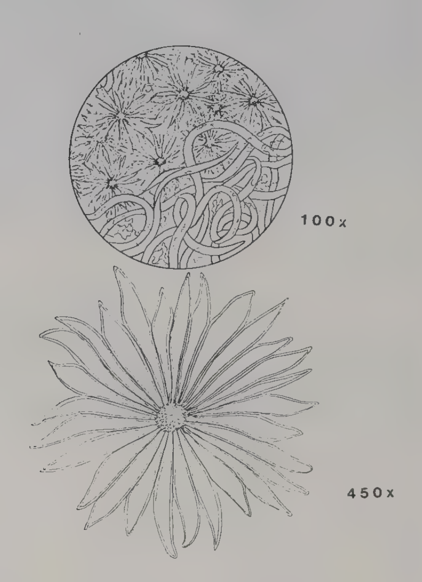


Fig. 4 – Stellate hair of a Meliaceae (*Melia azedarach*).

Fig. 4 – Vista agrandada de un pelo estrellado de una Meliaceae (*Melia azedarach*).

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SOCIAL PARASITISM IN YELLOWJACKETS

(VESPULA)

R.W. MATTHEWS

Department of Entomology – University of Georgia
Athens, Georgia 30602 U.S.A.

SUMMARY

Laboratory studies of competition between queens of two species of yellowjackets, *Vespula squamosa* and *V. maculifrons*, reveal that queens fight intensely over viable nests. Residents are more likely to win over intruders, despite unequal body sizes. The losing queen is fatally stung, but workers are killed by biting. Results are consistent with game theory which predicts intense contests for valuable resources (viable nests). Since orphaned workers may gain the opportunity to lay their own eggs their aggressive participation in queen battles may be interpreted as selfish. Data are presented on queen abundance, seasonal occurrence and habitat preferences based on sightings and Malaise trap collections. The possibility that social parasitism contributes to cyclical fluctuations in yellowjacket populations is considered.

RESUMEN

El parasitismo social en las avispas (Vespula)

Estudios en el laboratorio de competencia entre reinas de dos especies de *Vespula*, *V. squamosa* y *V. maculifrons*, revelan que las reinas pelean intensamente por nidos viables. Las reinas residentes frecuentemente ganan sobre las intrusas a pesar de un desigual tamaño del cuerpo. Tanto las obreras de nidos con reina como las que nos poseen reina, participan avidamente en las batallas. En este trabajo se presentan también datos de campo sobre la abundancia de las reinas, sobre su ocurrencia estacional y sus habitats preferidos, basados en observaciones y colectas con trampas Malayas.

INTRODUCTION

Four evolutionary «stages» of socially parasitic behavior have been hypothesized for yellowjackets (*Vespula* spp.) by Taylor (1939). The most advanced state is termed inquilinism, the case where host and parasite queen coexist for a period of time in the same nest and the parasite queen depends upon the host workers to rear its reproductives. An intermediate stage in the hypothetical evolutionary progression is represented by *Vespula squamosa* Drury, a common and widespread species in southeastern U.S. This species was regarded as a facultative temporary parasite of *Vespula maculifrons* Buysson (MacDonald and Matthews, 1975). I now believe that queens of *V. squamosa* are obliged to locate an embryonic nest of their host and usurp it, immediately killing the host queen (Matthews and Matthews, 1979). Ultimately, the host worker force is replaced by *V. squamosa* workers so that by mid-summer the colony becomes «pure» *V. squamosa*, having progressed through a temporary period when workers of both species coexisted. Facultative intraspecific usurpation also regularly occurs in both species.

Over the past few years I have been investigating the dynamics of *Vespula* queen behavior in Athens, Georgia, incorporating both field and laboratory studies. In the field, efforts have focused on determining queen abundance, queen flight seasons, nest initiation times and nest distribution over different habitats. Queen interactions in staged laboratory contests have provided insights into the behaviors of parasite and host. This paper presents some results of these studies.

METHODS

Field studies were conducted from late March through June annually from 1976 through 1979 in a municipal park in Athens, Georgia. A 300 m stretch of meandering stream flowing through a mature deciduous forest with an extensively cleared understory was the principal study area. The site was visited from one to three hours at least once daily, between 1000 and 1400 hrs and counts of all queens displaying typical nest searching behavior in the study area were made. Because none were marked, it is possible that some queens were sighted and counted more than once. An independent measure of queen abundance and activity was obtained by sampling with 3 Malaise traps (non-attractant collection devices that intercept flying insects), noted for their ability to catch Hymenoptera (Matthews and Matthews, 1970). One trap was placed in each of 3 contrasting habitats and emptied every other day. Habitats trapped included the municipal park, a botanical garden forest and a suburban back yard.

Embryo nests of *V. maculifrons* were excavated from their natural sites and re-established in observation boxes in the laboratory. The plywood nest boxes (35 x 35 x 4 cm) were fitted with removable glass bottoms and fronts. Adjustable mirrors positioned below the nest boxes allowed the observation of nest activities with minimal interference. Following a confinement period of 24 to 48 hr during which honey was provided, nest inhabitants were allowed access to the outside via flexible transparent tubing. Wasps reoriented readily and soon resumed normal foraging and nesting activities. Nests were maintained at room temperatures, humidity in the nest boxes was increased by the addition of a dish of saturated sand in one corner.

Field-caught searching queens of both species (each distinctively marked with paint) were introduced into nest boxes having reestablished colonies. Most experiments were conducted the same day that the introduced queen was caught, but in a few cases the introduced queen was chilled overnight. Introductions were made by placing the marked queen into a specially constructed plexiglass chamber connected midway along the entrance tube. A pair of one-way gates detained the queen and prevented her from escaping. Eventually the introduced queen found her way into the nest box and discovered the host nest more or less naturally. Interactions between residents and intruders were recorded on videotape for subsequent analysis.

RESULTS

Field studies . Queen occurrence and abundance

Table I gives the results of the Malaise trap collections of *Vespula* queens for 3 successive seasons. Although total numbers trapped are low, they suggest that queens of *V. squamosa* may be more restricted to disturbed and open habitats such as typified by suburban back yards. No *V. squamosa* were captured in the undisturbed forest of the botanical garden during the 3 years. In contrast, *V. maculifrons* queens were trapped in all habitats sampled and were about equal in abundance to *V. squamosa* in the suburban yard samples. Over the 3 seasons 544 *V. maculifrons* queens were sighted at the semi-natural municipal park study site compared to 50 *V. squamosa* queens (based on 188 observations hrs.), corroborating the Malaise trap findings.

Seasonal abundance of the two species based on Malaise trap collections is depicted in Fig. 1. Queens of *V. maculifrons* appear about one week earlier in the spring and are very abundant in early April with only an occasional queen taken later. In contrast *V. squamosa* queens appear later and exibit no clearly defined abundance peaks. An independent sample of queens from the spring of 1976 (Fig. 2) taken at a research station in Eatonton, Georgia (about 50 miles south of Athens) using Manitoba horse fly traps

Table I – Summary of *Vespula* queens captured by Malaise traps over three successive spring flight seasons in same locations in Athens, GA.

Tabla I – Resumen de reinas de *Vespula* capturadas con trampas Malayas durante 3 sucesivas estaciones de vuelo primaverales en las mismas localidades en Athens, GA.

Habitat	1976 Apr. 1 - July 4	1977 Mar. 15 - June 24	1978 Apr. 3 - May 30	Total
Municipal Park				
V. maculifrons	-	9	7	16
V. squamosa	-	1	1	2
Botanical Garden				
V. maculifrons	29	4	26	59
V. squamosa	0	0	0	0
Suburban Yard				
V. maculifrons	18	5	8	31
V. squamosa	20	6	1	27

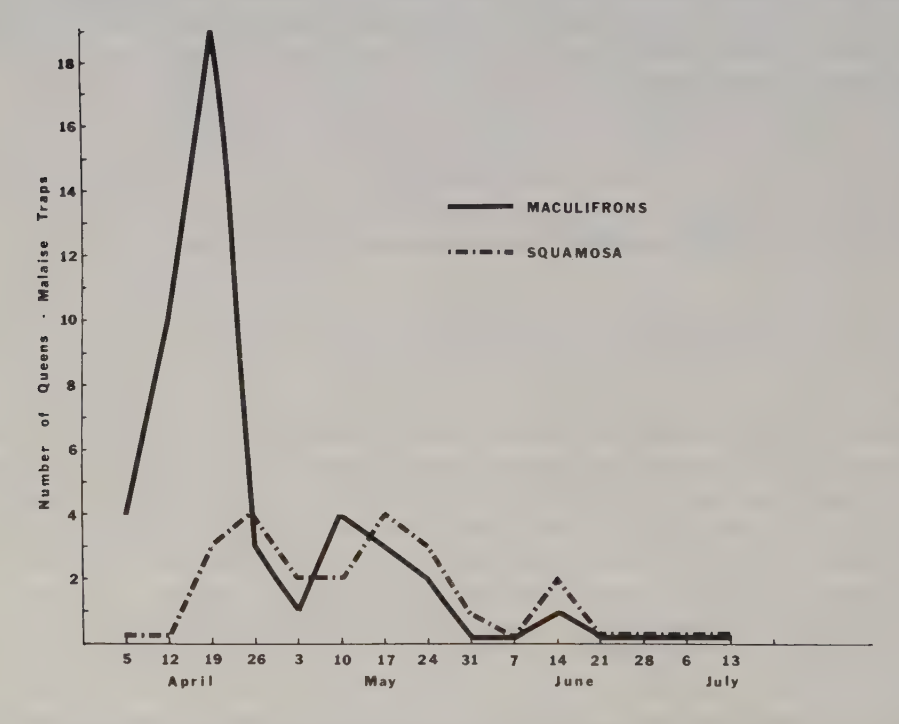


Fig. 1 – Seasonal abundance of *Vespula squamosa* and *V. maculifrons* queens throughout the queen flight season based on collections of Malaise traps in Athens, GA.

Fig. 1 – Abundancia estacional de las reinas de *Vespula squamosa* y *V. maculifrons* durante su vuelo estacional, basada en colectas con trampas Malayas en Athens, GA.

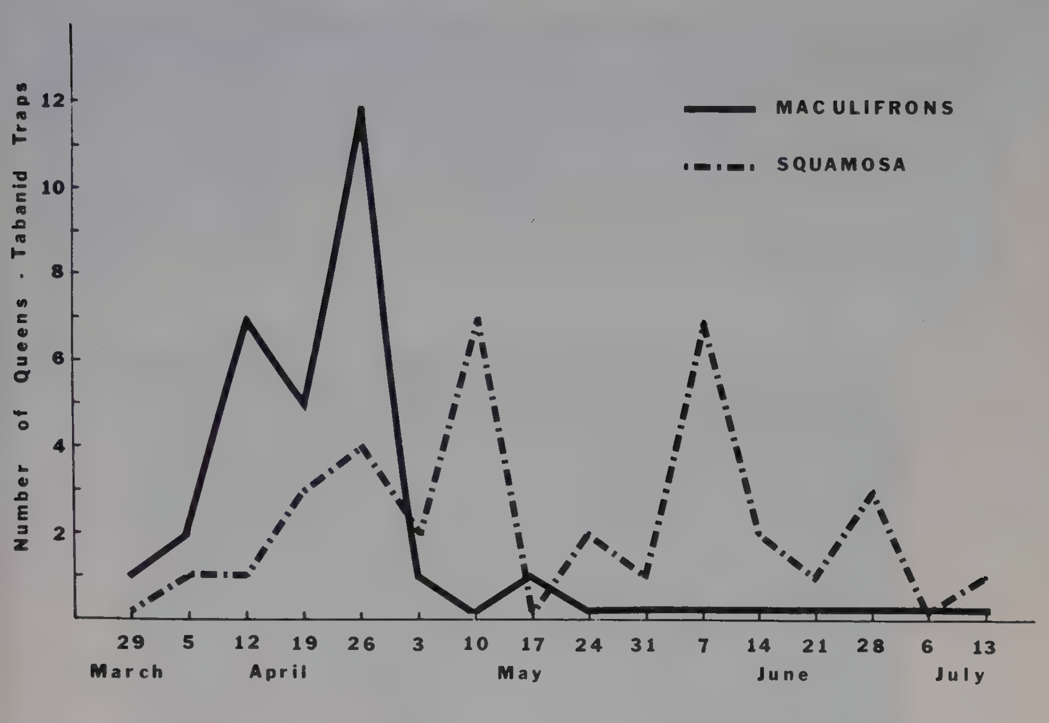


Fig. 2 – Seasonal abundance of *Vespula squamosa* and *V. maculifrons* queens taken in horse fly traps (see Thorsteinson et al., 1965) in Eatonton, GA.

Fig. 2 – Abundancia estacional de las reinas de *Vespula squamosa* y *V. maculifrons* colectadas en trampas para tábanos (ver Thorsteinson et al., 1965) en Eatonton, GA.

corroborates the Malaise collections. Additionally these data suggest that *V. squamosa* has a slightly longer flight season than does *V. maculifrons*.

Laboratory studies

Behaviors observed during agonistic interactions of *Vespula* queens included : search, approach, touch, bite, kick, sting, akinesis, retreat, and tumble. The sequence of these acts was highly variable and unpredictable in any queen contest. Workers (when present) also entered the fray and displayed a similar behavioral repertoire. Indeed, when workers were present they were usually the first to encounter an invading queen (Fig. 3). Invading queens did not use their stings in these encounters with workers, dispatching them instead by biting. The result was that workers were often dismembered

in these battles, and as many as 20 have been observed killed by an invading queen. Queens typically did not confront one another or fight for sometimes several hours after the alien entered the nest. The final confrontation typically took place inside the nest making it difficult to observe. On some occasions the embattled queens fell from the nest where they continued to grapple. Eventually one successfully stung her opponent, and the battle ended abruptly with the stung queen instantly paralyzed. Escalated contests also resulted in physical injury to one or both participants (see photos in Matthews and Matthews, 1979).



Fig. 3 – Orphaned workers of *Vespula maculifrons* mobbing an introduced *V. squamosa* queen (arrow) who has just invaded their nest in a laboratory nest box

Fig. 3 – Obreras sin reina de *Vespula maculifrons* atacando una reina de *V. squamosa* introducida (flecha) que ha recientemente invadido su nido, bajo condiciones de laboratorio.

Possible parameters thought to affect the outcome of queen contests included : (1) home bias, (2) relative size of combatants, (3) duration of interaction, and (4) presence of workers. Although sample sizes were small, home bias appeared to be the major determining factor (Table II). In 13 of 16 trials, regardless of species combinations, the resident queen prevailed. This difference is significant (p = .002, Fisher's Exact Probability Test). Despite the greater size of *V. squamosa, V. squamosa* queens won in only-third of its' contests. Workers in orphaned nests were highly aggressive toward intruders. Introduced queens were quickly mobbed by the workers who attempted to bite and sting, sometimes in a battle so intense that the nest was severely damaged. In only 4 of 13 trials did the introduced queen ultimately prevail (Table III).

Table II – Results of 16 staged *Vespula* queen contests using queen-right colonies

Tabla II – Resultados de 16 experimentos de introducción de una nueva reina de *Vespula* en colonias con reina.

Intruder Species	Fate of Intruder Queen	Opponent Resident Species		
		V. maculifrons	*V. squamosa*	Totals
V. maculifrons (n = 6)	Wins	0	0	0
	Loses	5	1	6
V. squamosa (n = 10)	Wins	2	1	3
	Loses	4	3	7

Table III – Results of 13 trials using orphaned colonies with variable numbers of workers present in which either conspecific queens or queens of a different species were introduced.

Tabla III – Resultados de 13 experimentos usando colonias huérfanas con número variable de obreras, en las cuales fueron introducidas reinas conespecíficas o reinas de una especie diferente.

	Intruder		
Outcome	Conspecific	Different species	Totals
Intruder wins	3	1	4
Intruder loses	6	3	9

Not revealed in these data is the fact that even the «winners» were sometimes ultimately losers ! Two successful defenders and two successful usurpers subsequently died of battle injuries, which under natural conditions would leave orphaned colonies, which, unless subsequently adopted, would be destined to die prematurely. Thus, there exists a small but measurable probability that any usurpation attemps will result in an orphaned nest.

DISCUSSION

Yellowjacket queen competition is essentially a contest situation which is *asymmetric* in the sense of Maynard Smith and Parker (1976). The payoff – possession of an established nest – has greatly different values for each contestant. The resident queen stands to lose her entire (and considerably greater) investment if she is defeated. The intruder on the other hand stands to gain a great deal by taking over, and (providing she survives to try again) will be little worse off in losing than if she had made no attemps at all. Under such asymmetric payoff conditions, Maynard Smith and Parker predict an intense «escalated» contest carrying the possibility of serious injury, even death, to one or both contestants. This is exactly the case in *Vespula* queen interactions. For yellowjacket queens the situation is exacerbated since contestants would seem to have no means of accurately assessing the fighting ability or resource holding power (RHP) of opponents in conventional ways. Animals fighting over territories are, for example, able to assess one another by various sorts of displays made in close proximity, but without physical contact. For example, fumel web spiders assess RHP of opponents via tactile stimuli perceived at a distance through the web. Most intense fights occur between roughly equal-sized individuals (Reichert, 1978). Decisions to escalate or withdraw can be made at a safe distance and escalated contests occur only when opponents are about evenly matched. This is not the case for *Vespula* queens who would seem to have no obvious way of predicting the situation underground in advance.

The staged laboratory queen contest outcomes suggest that the resident queen will usually hold the advantage. The relatively few documented cases of usurpation in nature (Mac Donald and Matthews, 1981) corroborate these data, suggesting that home bias may be an important factor under natural conditions as well. However, sighting records and queen trapping results from the field presented here suggest that there are seasonal as well as spatial aspects to queen competition which were not mimicked in the laboratory. Also, previous field studies showed that successful *V. squamosa* usurpation did not occur until after several *V. maculifrons* workers were present, with usurped nests averaging over 200 cells (Mac Donald and Matthews, 1975). Laboratory contests were staged with smaller nests containing up to about 60 cells and at most 15 workers.

Workers, being reproductively sterile, might be predicted to have little interest in a contests'outcome. Indeed, at first, I postulated that workers (particularly those in orphaned nests) should readily accept an invading queen since her presence would likely assure the perpetuation of an otherwise doomed colony. Experiments showed otherwise (Table III). A possible

explanation of worker pugnacity was suggested when some queenless nests began to produce males. In such nests, workers have a «once in a lifetime» chance to contribute their genes directly to the next generation. Acceptance of a foreign queen forfeits this opportunity. Hence from the workers standpoint, hostility toward invading queens is to be expected, even in queen-right colonies, though not necessarily for altruistic reasons. Conceivably some worker-derived males could live to mate.

On a larger time scale the aggressive interactions of queens may help to explain the cyclical nature of yellowjacket population fluctuations. Every year certain regions report high densities of yellowjacket populations (Akre and Reed, 1981) while in the subsequent year or two they seem to be hardly noticeable. Factors causing tremendous population fluctuations of yellowjackets are undoubtedly multiple and complexly interrelated (also reviewed by Spradbery, 1973 and Archer, 1980b). However, the results of this study suggest that queen warfare may play a larger role in population fluctuations than generally thought. The following scenerio is suggested. Consider first the situation where populations are high, and large numbers of fertile queens are produced to overwinter. Assuming that mortality due to overwintering is density independent (Archer, 1980b, gives a figure of 98 % winter mortality), the following spring the incidence and intensity of queen interactions would be relatively high, with a concommitant increase in nest failure rate due to repeated queen usurpation attempts (both intra-and-interspecific) each carrying the risk of severe damage and the possibility of being orphaned. Conversely, when overwintering populations are relatively low there would be a reduced probability of repeated nest disturbance by intruding queens the following spring, and hence a greater likelihood that a given nest will survive beyond the critical embryonic stage. Thus in seasons following low population densities, the fewer surviving queens may enjoy a greater probability of successful nest establishment and hence yellowjacket populations begin to build. Archer (1973, 1980a, b) has made a similar suggestion based upon his long term studies of British yellowjackets. Thus, the biggest single factor determining yellowjacket nesting success may not be the number of available nest sites or favorability of hibernating conditions or spring weather, but rather the abundance and behavior of other queens. To be sure, the vagaries of spring weather also impose their effect and impede our ability to accurately predict yellowjacket populations (Akre and Reed, 1981).

Clearly, the ability of a yellowjacket queen to initiate and defend a nest carries a very large risk. Perhaps, as Evans (1975) has said «... too much has been made of the sting as a defense against vertebrate enemies, and too little made of the sting as a means of repelling foreign queens».

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THE AFRICANIZED HONEY BEE

Round Table presided by Charles D. Michener

INTRODUCTION

The populations of honey bees (*Apis mellifera*) found in the tropical and subtropical parts of the New World, and derived at least in part from bees introduced from Africa (*Apis m. scutellata*, formerly called by the name of the West African race *A. m. adansoni* ; Ruttner, 1976) are widely called Africanized honey bees. The name Brazilian honey bees has also been applied to them.

Bees from Africa were introduced into Brazil in 1956 in order to develop a tropical – and subtropical – adapted strain having better honey productivity than the temperate European subspecies previously used in Brazil. Queens that reached Brazil were mostly from Pretoria, South Africa (over 1500 m altitude, 26°S, therefore an area with cool winters), but one was from Tabora, Tanzania. Colonies showing desirable characteristics were to be selected from among hybrids resulting from crosses of European and African bees. However, in 1957, 26 queens mated in Africa escaped with swarms or absconding colonies near Rio Claro, São Paulo, Brazil. The queen from Tanzania was among those that escaped (W.E. Kerr, in letter to O.R. Taylor, June 14, 1974).

The subsequent spread of bees of African origin or of hybrids between European and African races has been described in a review by Michener (1975) and a subsequent report by Taylor (1977). In recent years Africanized bees have rapidly spread across Venezuela and eastern Colombia, and no doubt will cross the Colombia-Panama border in the first half of 1981 and may reach the Panama Canal area in 1982 (O.R. Taylor, personal communication). Thus Africanized honey bees now occur in all parts of South America east of the Andes and north of about latitude 33°S. They do not appear to have extended their range much farther south than indicated by the authors cited above, perhaps because of cold winters, and they have not crossed the Andes into Chile or western Peru and Ecuador. They appear to spread more rapidly and develop larger populations in the savannas, cerrados, caatingas, and llanos, i.e., in relatively dry zones, than in the tropical forests.

There is no need to repeat here the records of mass stingings of animals and people by Africanized bees, with resultant deaths of some people and thousands of domestic animals, especially in Brazil and Venezuela. It is important to note that beekeepers have learned to manage these bees, especially in southern Brazil where hybridization with European bees may have

been significant, that high honey yields are reported, and that stinging incidents at least in the southern part of the range now appear to be uncommon in spite of large feral populations of Africanized bees.

The rapid spread of an aggressive new form is always a subject of interest. In this case it changed the race of *Apis mellifera* in areas where European races were already present, and in the tropics, where European bees were rare or absent, it added a species to an already extremely complex environment. The result has been a series of studies on the behavioral and ecological attributes of Africanized honey bees, comparisons between such attributes and those of European races, and studies of the impact of honey bees on tropical plants and their native pollinators.

This round table was organized to provide for discussion of biological and practical problems associated with the spread of Africanized honey bees, and to present a sample of recent investigations of these bees. The following authors and topics were included :

1. Mark L. Winston – Simon Fraser University, Vancouver, B.C., Canada – Life-history and Demographic Characteristics of the Africanized Honey Bee.
2. Gard W. Otis – University of Kansas, Lawrence, Kansas, U.S.A. – Swarming and Population Dynamics of the Africanized Honey Bee.
3. Orley R. Taylor – University of Kansas, Lawrence, Kansas, U.S.A. – Mating Biology of Africanized Honey Bees.
4. Josué A. Núñez – Instituto Venezolano de Investigaciones Cientificas, Caracas, Venezuela – Foraging Behavior of Africanized vs. European Bees.
5. David W. Roubik – Smithsonian Tropical Research Institute, Balboa, Panama – Competition of the Africanized Honey Bee with other Species.
6. Thomas E. Rinderer – U.S. Department of Agriculture Bee Breeding and Stock Center Laboratory, Baton Rouge, Louisiana, U.S.A. – Genetics of Defense Behavior in Honey Bees. (This paper was not presented orally).
7. Lionel S. Gonçalves – Dept. de Genetica, Faculdade de Medicina, Ribeirao Preto, S.P., Brazil – Effects of Climate on Behavior of Africanized Bees.
8. Antonio Zozaya – Direccion General de Apicultura y Especies Menores, Ciudad de México – Probable Impact of Africanized Bees in Mexico and Central America.

Certain of the papers listed above are printed here. The first is in press elsewhere (Winston et al., 1981) and will not be repeated here. Number 3 and probably number 8 will be presented in reorganized and more detailed form elsewhere.

I wish to thank all the authors for their contributions.

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Charles D. Michener
University of Kansas
Lawrence, Kansas 66045 U.S.A.

POPULATION BIOLOGY OF THE AFRICANIZED HONEY BEE

G.W. OTIS*

Department of Systematics and Ecology
University of Kansas, Lawrence, Kansas 66045 U.S.A.

SUMMARY

The birth rate, death rate, and population growth rate of unmanaged colonies of Africanized honey bees were determined in French Guiana. The study was undertaken to better understand the factors contributing to the rapid range expansion of the Africanized bee in South America. Colony fecundity was high. Colonies produced a mean of 2.82 swarms (range of 1-5) per swarming sequence. Mean swarm-to-swarm intervals were short : 49.9 days (n = 19) for colonies undergoing their first swarming sequence, and 72.4 days (n = 19) for colonies in their second or third swarming sequence. Because generation lengths were generally short, colonies founded early in the reproductive season underwent several swarming sequences per year. Losses of study colonies were also high due to predation (30 % loss of established colonies per year ; high mortality of small swarms immediately after colonization), loss of queens on mating flights (7.8 % per swarming sequence), and absconding (30 % per year). The median survival of established colonies was only approximately 7 months. With the aid of a computer simulation, colony births and deaths were integrated to yield a realized annual population growth rate of 16, a particularly high rate for honey bees. Historically, Africanized honey bees have attained high colony densities only 2-3 years after colonizing new regions. This pattern can now be more readily interpreted.

*** Present address : Department of Environmental Biology, University of Guelph, Guelph, Ontario NIG 2 W1, Canada.**

RESUMEN

Biología de Poblaciones de la Abeja Africanizada

Se determinó la velocidad de nacimiento, velocidad de muerte y velocidad de crecimiento de colonias no manejadas de abejas africanizadas en Guayana Francesa. Se hizó este estudio para una mejor comprensión de los factores que contribuyen a la rápida expansión del rango de la abeja africanizada en Sudamérica. La fecundidad de la colonia fué alta. Las colonias produjeron un promedio de 2.82 enjambres por secuencia de enjambrazón.

Los intervalos promedio de enjambre a enjambre fueron cortos : 49.9 dias (n = 19) para colonias que experimentaron su primera secuencia de enjambrazón, y 72.4 días (n = 19) para colonias en su segunda o tercera secuencia de enjambrazón. Las colonias fundadas tempranamente en el período reproductivo experimentaron varias secuencias de enjambrazón por año, debido a que los períodos de duración de las generaciones fueron generalmente cortos. Las pérdidas en las colonias de estudio fueron también altas debido a predación (30 % de pérdida en colonias establecidas por año ; alta mortalidad de pequeños enjambres inmediatamente después de la colonización), pérdida de reinas en vuelos nupciales (7.8 % por secuencia de enjambrazón), y evasión (30 % por año). La sobrevivencia media de colonias establecidas fué de aproximadamente sólo 7 meses. Con la ayuda de una simulación en computadora, se integraron nacimiento y muerte de las colonias para producir una velocidad de crecimiento poblacional anual de 16, velocidad particularmente alta para abejas melíferas. Historicamente, las abejas africanizadas han alcanzado altas densidades de colonias sólo después de 2 a 3 años de haber colonizado nuevas regiones. Este patrón, ahora, puede ser más facilmente interpretado.

INTRODUCTION

This paper summarizes research conducted on the population biology of the Africanized honey bee. African honey bees (*Apis mellifera scutellata* Ruttner, 1976) escaped from an apiary near Rio Claro, Brazil, in 1957, and the swarms produced by them and possible hybrids with European honey bee races have colonized most of South America (Kerr, 1967 ; Taylor, 1977), reaching very high densities in some areas. In order to better understand the rapid spread and growth of this feral population, unmanaged feral colonies were studied to document rates of swarming, absconding, mortality, and to determine generation lengths. This information has been used to model growth rates for a feral population in the savannas of coastal French Guiana.

Methods

This study was conducted from February 1976 to June 1977 in the savannas near Kourou, French Guiana, 5°10'N, 52°40'W. Hoock (1971) described the climate and flora of the region. Feral Africanized honey bee colonies were founded by trapping swarms with pressed-pulp swarm-boxes baited inside with a thin coat of beeswax (Taylor and Otis, 1978). These colonies were transferred to 22 litre hives that contained 6 movable top bars. Alternatively, some colonies were initated by placing swarms in 22 litre hives containing top bars fitted with a median strip of foundation that served as a guide for comb building. Otherwise, colonies built all their own comb. After successful establishment, colonies were left unmanaged except for hive inspections. The hives were placed along forest-savanna interfaces, usually in shade. No more than 10 colonies were ever located in an apiary, and each of the 11 apiaries was a minimum of 2 km from the next.

All colonies were inspected every 1-3 weeks for survivals, absconding, and swarming. Detailed swarming histories and swarm-to-swarm intervals were obtained by inspecting hives every day, or occasionally every second day, from the time first eggs were laid in queen cups until all queens had emerged from queen cells or had been destroyed naturally. The condition of each queen cell was recorded during inspections. Each comb was searched twice for queens, and all queens were marked with a numbered, color-coded label (Honig Mungesdorff, Postfach 290292, West Germany). The hive was weighed. When possible, swarms that issued from study colonies were caught, their sizes determined, and they were used to initate new study colonies. If not observed directly, swarms were determined to have issued by the loss of a marked queen and a concurrent reduction in hive weight ; usually there was also an obvious reduction in the worker population of the hive. This method detected all but a few of the smallest swarms (0.1-0.2 kg, 1,000-2,500 bees). After the completion of swarming, the parent colony was checked to determine if the new queen successfully mated and when she initated oviposition. More detailed methods are presented by Otis (1980). The choice of the 22 litre hive design proved to be fortuitous. The mean volume occupied by feral colonies in Peru which had initated queen rearing or had swarmed once was 23.3 litres (n = 10 ; Winston and Taylor, in press). Feral nests measured in French Guiana were comparable in size.

All bees studied were Africanized. Feral honey bees were not present in French Guiana prior to the arrival of Africanized bees in 1974 (Otis and Taylor, 1980). The only colonies of European honey bees had been located in Cayenne, 48 km southeast of Kourou. All 15 of these colonies had become Africanized by the time this study was initiated (determined behaviorally through personal observations and confirmed by morphometric analyses by H. V. Daly). No other managed colonies of honey bees were maintained within 200 km of the study area. Morphometric analyses of workers taken from many study colonies confirmed that the bees were Africanized with no evidence of recent hybridation (H. V. Daly, pers. com. ; Daly and Balling, 1978).

RESULTS

Honey bees reproduce by swarming. In a normal swarming sequence, fertilized eggs are laid in special queen cups. Six to 30 days later, usually after at least one queen cell has been sealed, the queen leaves with a large group of workers from the colony. Approximately eight days after the first queen cell has been sealed, the first virgin queen emerges. She then either destroys the remaining queen cells, mates and initiates ovipositions, or she leaves with a smaller group a workers in what is known as an afterswarm (cast). The afterswarming process can be repeated with new virgin queens several times before one of the last queens to emerge kills the remaining queen brood (in cells), mates, and initiates egg laying.

A non-reproductive swarm is produced when a colony absconds, or abandons its hive. This is also sometimes referred to as a migratory swarm (Chandler, 1976). Absconding differs from reproductive swarming in that the colony produces no new queens and the entire population of workers leaves its nest with the mated queen. Reproductive swarming was common from August 1976 through February 1977. Nearly all colonies swarmed at least once during this period. As swarming frequency declined in March, absconding frequency increased, reaching a maximum in mid-April and declining again in May. A minor period of absconding also occurred in early October. Subsequent to this study, swarming and absconding continued at a lower level from July to December 1977 (P. Kukuk, pers. obs.). In the 39 detailed swarming sequences studied, each colony produced from one (prime swarm only) to five swarms (prime swarm and four afterswarms). The frequency distribution of afterswarm production is given in Table I. Colonies produced a mean of 1.85 afterswarms per swarming cycle. Three colonies (3 % n = 84) failed to produce prime swarms, but produced virgin queens and underwent a normal afterswarming process. On the average, a colony that swarmed produced 0.97 prime swarms and 1.85 afterswarms, as well as continuing to exist itself, thereby yielding a gross total of 3.82 colonies and swarms per swarming sequence.

During the swarming season from August 1976 to March 1977, colonies had rapid growth rates and short generation lengths (Table III). Colonies founded by swarms with 10,000 or more workers in empty hives produced reproductive swarms a mean (harmonic) of 49.9 days later (n = 19). A few swarms reproduced in less than 35 days. Colonies which had already swarmed at least once had a mean prime swarm to prime swarm interval of 72.4 days (n = 19). Part of this latter interval was spent in completing the afterswarming process and in queen mating. Excluding the time involved in afterswarming and mating, the mean interval from the resumption of oviposition until issue

Table I – Numbers of afterswarms produced in 22 liter hives by Africanized honey bee colonies per swarming sequence.

Tabla I – Número de enjambres secundarios producidos por colonias de abejas africanizadas en colmenas de 22 litros por secuencia de enjambrazón.

Number of afterswarms	0	1	2	3	4	
Frequency	5	10	14	6	4	$\Sigma = 39$
Total afterswarms produced	0	10	28	18	16	$\Sigma = 72$
Mean afterswarm production						1.85 ± 0.186

Table II – Mortality of recently colonized swarms of differing sizes resulting from attacks of ants (*Camponotus* sp.).

Tabla II – Mortalidad de enjambres de diferentes tamaños recientemente colonizados resultante de ataques por hormigas (*Camponotus* sp.).

Swarm Size	Probability of death	n
1.00 + kg	0.00	13
0.75 - 0.99 kg	0.20	5
0.50 - 0.74 kg	0.33	3
0.25 - 0.49 kg	0.50	6
0.0 - 0.24 kg	0.66	3

of the next prime swarm was 59.7 days (n = 19). These short generation lengths allowed some colonies to undergo as many a four swarming sequences per year. Smaller swarms (e.g., many afterswarms) required more time to attain the conditions that induce swarming.

In conjunction with a high colony birth rate, colonies also had a high death rate. The period of greatest risk for a colony was during and just after swarming, when the worker population was low and the queen was mating. The sources and magnitudes of mortality are enumerated below. At the end of a swarming sequence, the remaining virgin queen leaves the colony to mate. During mating flights, queens are vulnerable to predation by birds (e.g., tyrant flycatchers), dragonflies, and other bee predators. In this study, 7 of 90 (7.8 %) queens disappeared at the time of mating. Virgin queens in afterswarms may sustain a similar rate of mortality leading to the «death» of their swarms. After having issued from the parent colony, a swarm scouts for and colonizes a new domicile. Many swarms undoubtedly die through starvation or predation by ants before successfully establishing new nests, but quantifying this source of mortality is difficult. Mortality occurring between swarm issue and colonization could not be estimated. Swarm mortality from ant attacks (*Camponotus* sp.) immediately after colonization was quite high

and related to swarm size (Table II). For example, no swarm weighing more than 1.25 kg died at this time, but 50 % of colonies between 0.25 and 0.50 kg were killed.

Table III – Frequency distributions of generation lengths (in days) for Africanized honey bee colonies during the swarming season. A, from colonization to swarming intervals for newly founded colonies ; B, prime swarm to prime swarm intervals for established colonies in their second or third swarming sequence ; C, oviposition to prime swarm intervals for colonies in their second or third swarming sequence. X = harmonic mean, n = number of colonies observed.

Tabla III – Distribución de frecuencias de duración (en días) de generaciones para colonias de abejas africanizadas durante el período de enjambrazón. A, intervalos desde colonización hasta enjambrazón por colonias recien fundadas ; B, intervalos desde enjambre primario hasta enjambre primario por colonias establecidas durante la 2da o 3ra secuencia de enjambrazón ; C, intervalos desde oviposición hasta enjambre primario por colonias durante la 2da o 3ra secuencia de enjambrazón. X = medio armónico, n = número de colonias observadas.

Midpoint of Interval (days)	A	B	C
30	1	0	0
35	1	0	0
40	4	0	1
45	2	0	1
50	1	0	1
55	2	2	3
60	4	3	6
65	1	1	3
70	1	3	1
75	0	2	1
80	0	2	1
85	0	1	0
90	0	1	0
95	1	3	1
100	0	1	0
105	1	0	0
$\bar{X}$	49.9	72.4	59.7
n	19	19	19

A few established colonies were attacked by army ants or animals such as armadillos and tamanduas. Such colonies either died or were able to abscond, after which they again had to attempt to establish a new nest. The probability of such attacks on established colonies was 0.001 per day, or 30 per cent loss per year. Finally, 31 % of the colonies (n = 65) absconded between August 1976 and August 1977. During the major absconding period from March to May, absconding appeared to be a response to poor food resource conditions, but was also influenced by the recency of swarming (Winston et al., 1979). Three colonies which received direct sunlight absconded in early October, apparently as a result of colony overheating. The majority of colonies that absconded had the additional problem of having to establish a new nest during an unfavorable season.

A survivorship curve was constructed for established colonies. The periods survived by each colony, computed in half months, were determined from the time of successful colony establishment until the time of colony loss due to death or absconding. The proportion of colonies surviving in each age class after colony establishment was then determined and plotted (Fig. 1). Because of the duration of the study (1 1/2 years), longer colony survivorship are slightly under-represented ; the dotted line estimates the survivorship curve adjusted for this factor. Colonies generally were short-lived. After 7 months, only half the established colonies were extant. This survivorship curve is for established colonies only and does not include mortality that occurs in the nest-founding period.

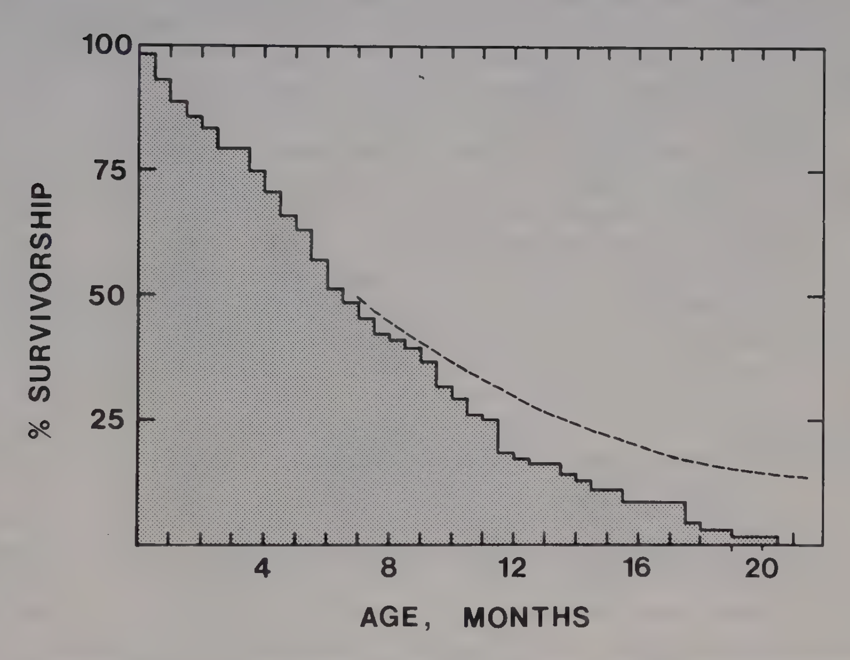


Fig. 1 — Survivorship curve for established colonies of Africanized honey bees. Losses were due to predation, absconding, and queen loss. Broken line represents an estimated survivorship curve based on the assumption that survivorship of longer lived colonies was underestimated during the study.

Fig. 1 — Curva de sobrevivencia de colonias establecidas de abejas africanizadas. Las pérdidas se debieron a predación, evasión y pérdida de la reina. La línea punteada representa una curva estimada de sobrevivencia basada en la suposición que la sobrevivencia de colonias de mayor longevidad fué subestimada durante el estudio.

It is evident that Africanized bees have both high reproductive rates and high mortality. In order to estimate the population growth rate, it was necessary to integrate births and deaths. Standard life table analyses were not applicable. It was not possible to accurately age many colonies, and swarming and absconding were not age-related events ; thus it was impossible to construct a current (time-specific) life table. It was also not possible to follow a cohort of colonies and construct an age-specific life table. Population projection matrix approaches could not be used because probabilities of some colony events (e.g. swarming) varied over time, and reproduction had neither an annual or constant-generation basis. Because of these difficulties, a unique computer simulation was developed. The simulation began with a single, established Africanized bee colony. That colony and all swarms derived from it were followed over a 318 day period analagous to the actual study interval for which sufficient data were available. The outcomes of all colony events and the time intervals between events were selected at random from the appropriate data sets generated in the field studies. The simulation outcome was the number of colonies alive at the completion of the simulation. Complete details of the simulation are given by Otis (1980).

The nature of the simulation was such that a nearly infinite number of patterns were generated. For example, the original colony could die before producing swarms, yielding a net number of colonies of 0. Alternatively, the initial colony could swarm early in the simulation, ultimately producing many surviving daughter and granddaughter colonies by the end of the simulation. A frequency distribution of the outcomes from 1,000 independent simulations is given in Fig. 2. A few simulations yielded more than 50 colonies, but most resulted in few surviving offspring. The mean outcome from these simulations was 15.17 (S.E. = 0.358) ; meaning that on the average, a colony started at the beginning of the study period would give rise to over 15 new colonies in 318 days. It was estimated that a population of 1,000 feral colonies would increase to 16,000 colonies during one year. This is an extremely high rate of increase.

In addition, the simulation was programmed to return the number of colonies alive at the beginning of each month in each simulation. The mean of these monthly values were plotted (Fig. 3). The resulting pattern parallels the general swarming and absconding pattern already described. The simulated population grew steadily throughout the swarming season (August through February) although the minor absconding period in October caused the slight reduction in growth. A peak of about 17 surviving colonies per colony was reached just prior to the major absconding season, after which the simulated population declined about 15 %. The gradual resumption of swarming in June caused the population to increase to the value of 15.2 colonies at the end of the study period.

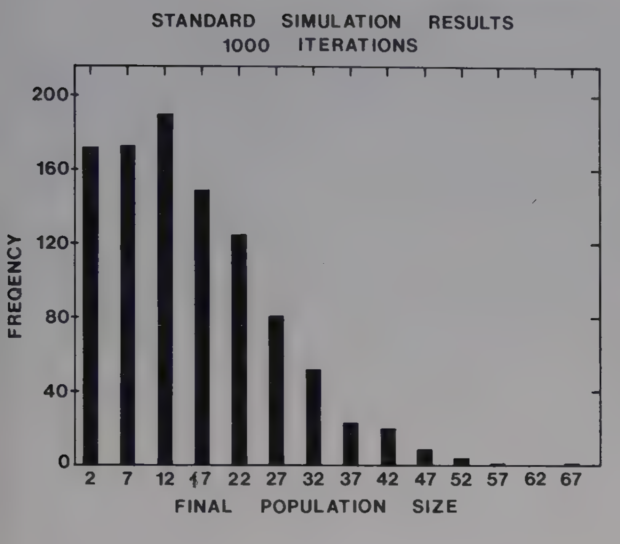


Fig. 2 – Frequency distribution of the colony population growth rates computed in 1,000 independent iterations of the simulation. The simulation was developed to analyze the population growth rate and pattern of feral Africanized bees.

Fig. 2 – Distribución de frecuencias de la velocidad de crecimiento de la pobalción de la colonia computada en 1,000 repeticiones independientes de la simulación. La simulación se desarrolló para analizar la velocidad y patrón de crecimiento de la población de abejas africanizadas silvestres.

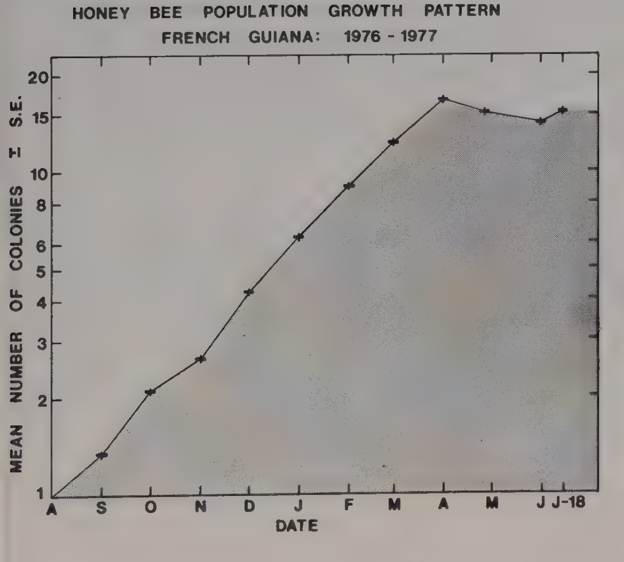


Fig. 3 – The simulated pattern of growth of the Africanized honey bee population for the 318 days interval of intensive study.

Fig. 3 – Patrón simulado de crecimiento de la población de abejas Africanizadas durante 318 días de estudio intenso.

DISCUSSION

The Africanized honey bee population in French Guiana was characterized by rapid intra-colony growth rates (Winston, 1979), small colony size, frequent swarming, production of numerous afterswarms, reproductive swarming during most of the year, absconding during adverse conditions, low colony survivorship, and an annual growth rate of 16 colonies per colony. The life history attributes of European races of honey bees in temperate regions (New York and Kansas, U.S.A.) contrast with this. Feral colonies of European bees are considerably larger ; mean comb area was 23,400 cm^2 (Seeley and Morse, 1976) vs. 8000 cm^2 for feral Africanized colonies in Peru (Winston and Taylor, 1980). They undergo one, or occasionally two, swarming sequences per year (Seeley, 1978 ; Winston, 1980). Slightly fewer afterswarms are produced (mean of 1.5 ; Winston, 1980), and few of these survive their first winter (Otis, unpublished data). Mean colony longevity was quite long, 2.1 years, and considerably longer, 5.6 years, for colonies that had successfully survived the first winter. The net reproductive rate was approximately equal to 1.0 (Seeley, 1978). The major selective force shaping these traits is the prolonged cold of winter. Relatively large colony size and good honey storage capabilities are selected for. Small swarms that cannot store much honey before winter have a low probability of survival (Otis, unpublished data).

The life history «tactics» of Africanized bees may be largely a response to predation, the major mortality factor observed in this study. In addition, colonies were free of the limitations imposed by a cold winter and did not require large stores of honey to survive. Under these conditions, frequent swarming at small colony size and the production of large numbers of swarms is a more successful strategy. Absconding, a rare behavior among European bees (Martin, 1963), then becomes a viable option during periods of resource scarcity.

In general, a consistent pattern of population increase has been observed for Africanized bees over most of South America. Initially, small numbers of swarms colonize regions, but within two or three years the feral colony density becomes very high. It has not been possible to understand this population phenomenon on the basis of our knowledge of the swarming process among European bees. Now, with the information concerning the frequency of swarming, numbers of afterswarms produced, and the annual population growth rate for Africanized bees in French Guiana, this growth process is more readily interpreted.

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COMPARACION DEL COMPORTAMIENTO RECOLECTOR DE ABEJAS AFRICANIZADAS Y ABEJAS EUROPEAS

J.A. NÚÑEZ

CBB – I.V.I.C., Apartado 1827,
Caracas 101, Venezuela

RESUMEN

Patrones de comportamiento recolector de dos líneas de *Apis mellifera, E.* de origen Europeo (variedad *ligustica*) y *A.* híbrido descendiente de variedades Africanas, muestran diferencias en duración de visitas, cantidad máxima de solución cargada en el buche y umbral de flujo de solución azucarada para la actividad de reclutamiento exhibida en el simulador (Fig. 1).

1. Las abejas *A* hacen visitas de recolección más cortas que las abejas *E* (Fig. 2) y consecuentemente transportan cantidades mas pequeñas de solución de azúcar que las abejas *E* ; sin embargo, la producción de miel de colmenas *A* es mayor que la lograda por las abejas *E* en el trópico.

2. Condicionadas a recolectar en un simulador dividido en dos grupos (Fig. 4), las abejas *A* mostrarón frecuencias de menor permanencia (tiempo gastado por una abeja en un grupo de alimentadores antes de cambiar a otro dentro de la misma visita) significativamente mayores que en las abejas *E* (Fig. 5). El tiempo gastado en una fuente alimenticia dada, parece ser menor para las abejas *A* que para las abejas *E.* Las abejas *A* permanecieron con fidelidad en un grupo de alimentadores sólo 60 % del tiempo que las abejas *E.*

3. El efecto transitorio del acortamiento de las visitas durante el primer viaje al simulador cuando imprevistamente se ofrece un flujo do oferta mayor, es más evidente en las abejas *A* que en las abejas *E* (Fig. 6a y 6b).

Los resultados son discutidos en base a que, para una ganancia óptima de la colonia, la abeja recolectora no sólo debe recolectar, sino también intercambiar información en la colmena acerca de la disponibilidad de azúcar en las fuentes que visita. Un incremento en la eficiencia de recolección podría alcanzarse por un alargamiento, en la duración

de la visita, pero para intercambiar información, un acortamiento en el tiempo del viaje recolector sería preferido. Los resultados obtenidos, tanto con la cantidad de solución cargada en el buche de abejas individuales, como con el éxito en el reclutamiento, sugieren que las abejas *A* estarían mejor adaptadas para una mayor vinculación informacional. Las diferencias conductuales observadas entre las dos líneas, *A* y *E*, concuerdan bien con las características que diferencian los biótopos donde se originaron las líneas : templado y tropical. Las dos peculiaridades más sobresalientes del biótopo tropical son la mayor riqueza en *diversidad floral* y un mayor *flujo de solución azucarada* por flor. Ante la riqueza en número de especies de plantas, las abejas *A* estarían mayor adaptadas que las abejas *E* por poseer un canal de información con una mayor capacidad para transmitir cambios frecuentes de fuentes alimenticias. El mayor flujo de solución azucarada en el trópico se compensaría con los mayores requirimientos energéticos de la abeja que se mueve a una mayor velocidad entre las fuentes que explota, alcanzando así una mayor capacidad de recolección.

SUMMARY

Comparison of foraging behavior of Africanized and European Bees

The foraging behaviour patterns of the two strains of *Apis mellifera, E*, of European origin (*ligustica* strain) and *A*, hybrid descendants from African strains, show differences in lenghts of visits, the maximal crop load and the sugar flow threshold for recruiting activity displayed at a simulator device (Fig. 1).

1. *A* bees make shorter foraging trips than *E* bees (Fig. 2) and consequently transport smaller loads of sugar solution than *E* bees ; nevertheless, honey yields of *A* hives are greater than those achieved by *E* bees in the tropics.
2. Conditioned to forage on a two patch simulator (Fig. 4), *A* bees showed a significantly greater frequency of shorter bout times (time spent by one bee at a group of feeders before moving to another within the same visit) than *E* bees (Fig. 5). The time spent at a given food source seems to be less for *A* than for *E* bees. *A* bees remained faithful to a patch of feeders only 60 % as long as *E* bees.
3. The transient shortening of visits during the first trip to the simulator when an unexpectedly high rate of flow is offered, is more evident in *A* than in *E* bees (Fig. 6a & 6b).

Results are discussed on the basis that, for optimal gain of the colony, the foraging bee must not only forage but also exchange information in the hive about the availability of sugar on food sources. An increase in foraging efficiency would be attained by lenghtening the duration of the visit, but for information exchange shortening of the trip would be preferred. Results obtained, both with crop load of the individual bee as well as success of recruiting, suggest that *A* bees would be better adapted for greater information exchange.

The behavioural differences observed between the two strains, *A* and *E*, match well with differences known to characterize the biotopes where the strains originated : temperate and tropical. Two outstanding peculiarities of the tropical biotope are greater richness in *floral diversity* and greater *sugar flow* per flower. In the face of this richness of plant species, the *A* bee would be better adapted than the *E* bee by possessing an information channel with greater capacity to transmit frequent changes of feeding place. The greater sugar flow in the tropics would compensate for the greater energetic requirements of the bee that moves at a greater speed among sources, thereby attaining a greater gathering capacity.

INTRODUCCIÓN

Desde su importación en el año 1956, las abejas africanas y sus híbridos se han dispersado por el continente Sudamericano desplazando a abejas domésticas europeas en numerosas regiones y colonizando nuevas áreas hasta entonces sin abejas domésticas (Taylor, 1977). Considerando que uno de los factores determinantes de este éxito de las abejas africanizadas podría residir en diferencias de comportamiento recolector que permitan a las africanizadas obtener una mayor ganancia de alimento, se realizaron algunos ensayos comparativos en ambas líneas.

MATERIAL Y MÉTODOS

Las abejas utilizadas pertenecen a líneas de *Apis mellifera* (E) de origen europeo (*A. m. ligustica*) y (A) híbridos descendientes de abejas africanas (*A. m. adansonii*) mantenidas en el Departamento de Genética de la FMRP, Ribeirão Preto, S.P. Brasil. Los ensayos se realizaron durante los años 1972 y 1975, al finalizar la estación seca cuando la motivación recolectora es máxima debido a la escasez de fuentes de alimento naturales.

El dispositivo básico utilizado es un simulador (Fig. 1) compuesto de 12 alimentadores que reciben solución azucarada (sacarosa 50 %) de igual número de microburetas tipo Scholander (Núñez, 1971). Las buretas son accionadas por un motor sincrónico cuya velocidad determina el flujo (μl/min) de solución finalmente inyectado. El conjunto de los 12 alimentadores del simulador constituye la «fuente de alimento» explotada por la abeja. El dispositivo permite obtener flujos de solución entre 0.02 μl/min y 1 μl/min por alimentador lo que equivale a 0,24 μl/min y 12 μl/min para el conjunto de los 12 alimentadores de la fuente de alimento. Para igual flujo en la «fuente de alimento» no se observan diferencias significativas entre simuladores de 4 o 12 alimentadores que, a juzgar por el comportamiento de la abeja, serían equivalentes.

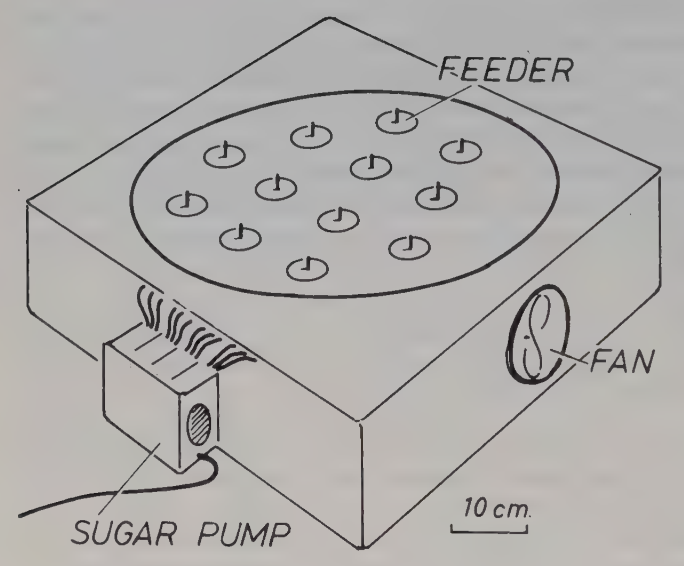


Fig. 1 – Food source simulator (First series of experiments).

Fig. 1 – Simulador de fuente alimenticia (primera serie de experimentos).

Para los experimentos se utilizaron colmenas ubicadas a una distancia de 50 metros del laboratorio. Las medidas se realizaron con abejas individuales condicionadas al simulador excluyendo cuidadosamente las nuevas reclutadas. El comportamiento recolector de la abeja condicionada al simulador es idéntico al que muestra en las fuentes naturales ; durante la visita vuela inspeccionando los alimentadores a razón de 7 a 10 por minuto recolectando la solución azucarada que halla en ellos. La visita termina cuando la abeja «decide» regresar a la colmena. Durante la primera visita de una serie a un nuevo flujo, el comportamiento puede ser diferente del que se observa para las visitas subsiguientes al mismo flujo. Para evitar este efecto transitorio no se considero esta primera visita al analizar los resultados.

RESULTADOS

1ra serie de experimentos

Se determinó la duración de la visita y la cantidad de solución cargada en el buche para diversos flujos de oferta en el simulador. Para todo el rango de flujos la abeja africanizada (A) realiza visitas de menor duración que la europea (E) (Fig. 2). Como consecuencia la cantidad de solución transportada por visita resulta correspondientemente menor (Fig. 3). Para flujos altos la diferencia (28,5 %) resulta de la diferencia de tamaño del buche, menor en la

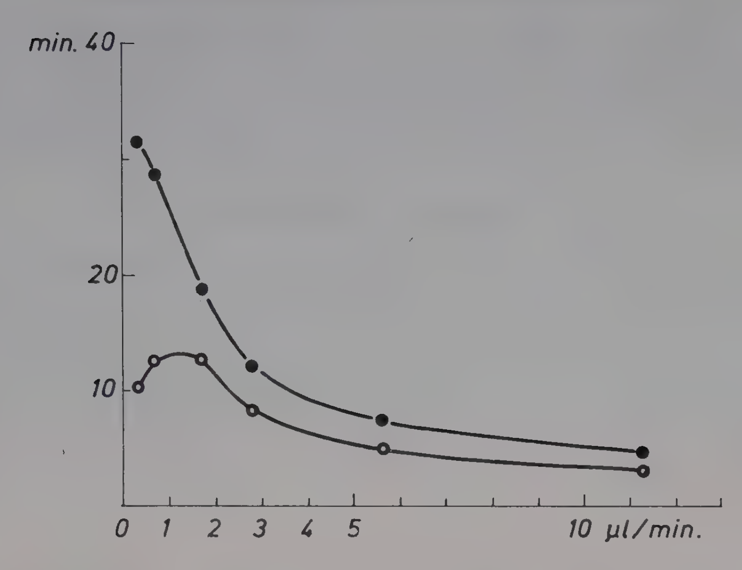


Fig. 2 – Visiting time (ordinate) for bees at different rates of flow (abscissa) of 50 % sucrose at the simulator. *A* bees (open circles) ; *E* bees (solid circles).

Fig. 2 – Duración de visitas ordenada por abejas a diversos flujos de oferta (abscisa) de sucrosa al 50 % en el simulador. Abejas *A* (círculos claros) ; abejas *E* (círculos oscuros).

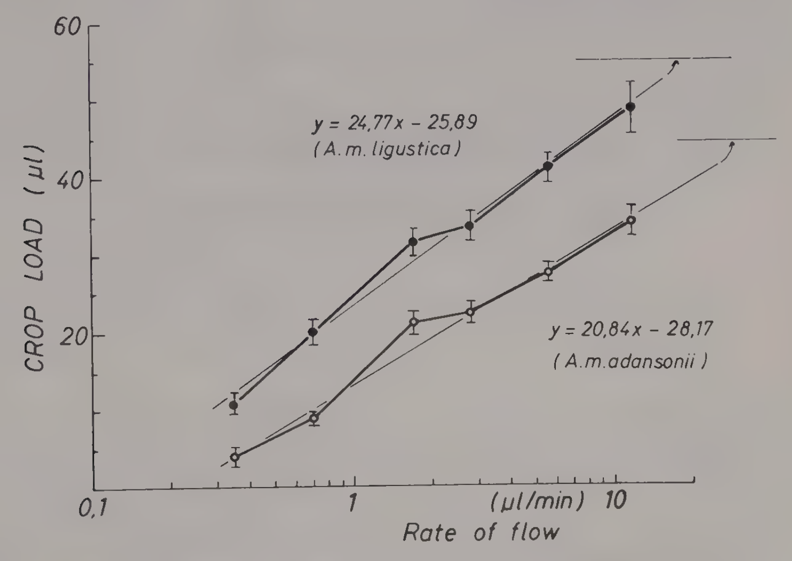


Fig. 3 – Crop load (ordinate) for different rates of flow (abscissa) of 50 % sucrose at the simulator. *A* bees (open circles) ; *E* bees (solid circles).

Fig. 3 – Cantidad de solución cargada en el buche (ordenada) para diversos flujos de orferta (abscisa) de sucrosa al 50 % en el simulador. Abejas *A* (círculos claros) ; abejas *E* (círculos oscuros).

(A) (Beig D., Pisani J. & Kerr W.E., 1972). Para flujos decrecientes esta diferencia aumenta y llega a ser 67,3 % menor en la A para el flujo de 0,7 μl/min (Núñez, 1974). Simultáneamente se observa que el umbral motivacional para reclutamiento se alcanza en la africanizada para mayor flujo que en la E.

2da serie de experimentos

El simulador fué dividido en dos grupos de 6 alimentadores cada uno (Fig. 4) a 1 metro de distancia uno del otro. La solución azucarada fué inyectada con un flujo de 1,2 μl/min, es decir 0,1 μl/min por alimentador. La abeja recolectora fué condicionada a recolectar de ambos grupos de alimentadores durante la visita. Se midió la duración de la permanencia en cada alimentador y por grupo de alimentadores. Para el segundo caso los resultados obtenidos se representan en la figura 5.

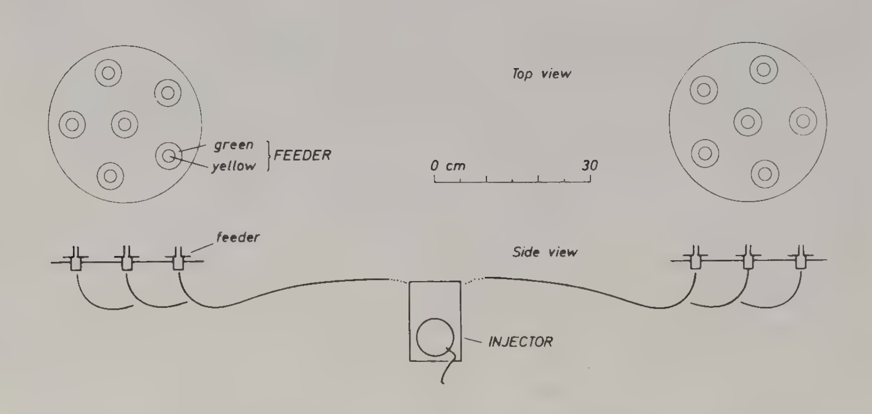


Fig. 4 — Two patch food source simulator (2nd series of experiments).

Fig. 4 — Simulador de fuente alimenticia dividido en dos grupos (2da serie de experimentos).

Con excepción de la permanencia de breve duración (0-50) mas frecuentes en la abeja A que en la E, no hubo diferencia significativa entre ambas abejas. La persistencia media para un grupo de alimentadores fué menor en la abeja A que en la E. Una estimación como persistencia o fidelidad relativa indica que las abejas A persisten recolectando sobre un grupo de alimentadores solo 60 % del tiempo que las abejas E (Núñez, 1979a).

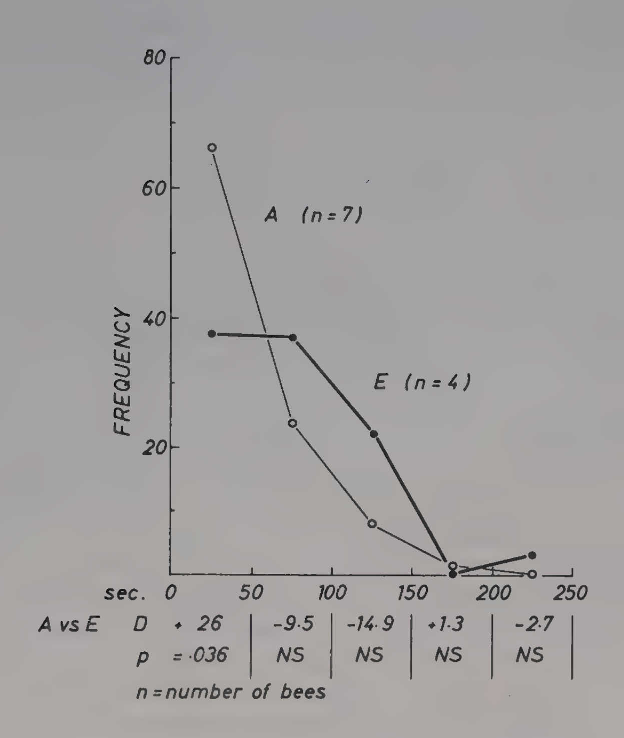
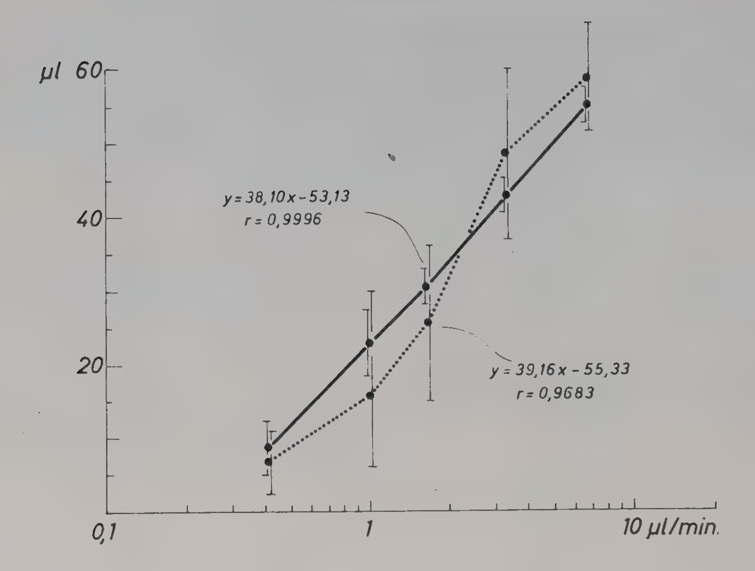


Fig. 5 — Frequency distribution of mean bout times. *A* bees (open circles) ; *E* bees (solide circles) ; P based on Mann-Whitney U-test ; n : number of bees.

Fig. 5 — Distribución de frecuencias de permanencia media. *A* abejas (círculos claros) ; *E* abejas (círculos oscuros) ; P basado en test-U de Mann-Whitney ; n : número de abejas.

3ra serie de experimentos

Como se señaló oportunamente, la duración de la visita y como consecuencia de la carga de buche presenta un efecto transitorio durante la primera visita a un nuevo flujo (Núñez, 1966). En una serie de ensayos se estudió este efecto transitorio utilizando un programa de ofertas al azar. Los flujos presentados fueron diferentes de visita en visita según una serie de números al azar. En esta modalidad el efecto transitorio está acentuado para los flujos extremos, altos y bajos. Los resultados se presentan en la fig. 6a y 6b. La diferencia más llamativa entre ambas líneas es la tendencia que muestra la



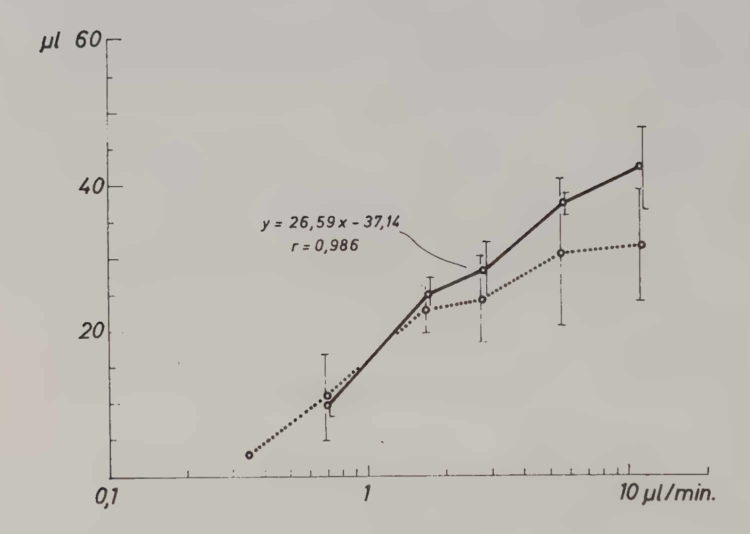


Fig. 6 – Crop load (ordinate) for different rates of flow at the simulator. Dotted line stands for at-random-program of rates of flow. 6a = *E* bees ; 6b = *A* bees.

Fig. 6 – Cantidad de solución cargada en el buche (ordenada) para diversos flujos de oferta en el simulador. La línea punteada representa un programa de ofertas al azar. 6a = abejas *E* ; 6b = abejas *A*.

abeja africanizada a disminuir la carga de buche para los flujos altos cuando la presentación es al azar. Es decir, a diferencia de las abejas E, las A muestran cierta tendencia a abreviar la duración de la visita cuando, de manera imprevista, se les presenta un flujo alto.

DISCUSION

Durante el viaje recolector, además del néctar la abeja obtiene información sobre la disponibilidad de alimento en las fuentes que explota. Al regresar a la colmena, junto con el alimento recolectado entrega información sobre la disponibilidad en la fuente visitada y recibe información sobre otras fuentes de alimento explotadas por la colmena.

El intercambio de información entre abeja recolectora y colmena se realiza con una frecuencia que depende de la distancia a que se encuentra la fuente de alimento y de la duración de la visita, pero además del número de abejas que explotan la misma fuente de alimento. Como al disminuir el flujo de solución en la fuente también disminuye el grado de repleción del buche (para flujos menores que 10 µl/min), el reclutamiento de novicias para una fuente en explotación permite aumentar la frecuencia de comunicación con la colmena. Tanto el efecto de reducir la carga con el flujo en la fuente como el de reclutar colaboradoras para la misma fuente, reducen el rendimiento recolector de la abeja individual pero aumentan la vinculación informacional entre colmena y abejas recolectoras. La menor duración de las visitas de las abejas A que las E para un mismo flujo, permitiría entonces, a costa de un menor rendimiento de la abeja individual, aumentar la vinculación informacional en la colmena A. Cuando el rendimiento relativo de una fuente es muy bajo la abeja que la explota permanece mayor tiempo en la colmena (Núñez, 1966) . El umbral para tal comportamiento se presenta en las abeja A para un flujo mayor que en las E. Las abejas A necesitan mayor flujo de oferta en el simulador para entrar en actividad.

La menor persistencia relativa sobre un alimentador o grupo de alimentadores (Fig. 5) es una característica que diferencia a las abejas A de las E. Esta diferencia de comportamiento en condiciones naturales cuando el número de alimentadores (flores) es muy elevado permitirá a la abeja A alcanzar mayor flujo de recolección. La diferencia relativa de persistencia sobre un grupo de alimentadores para el flujo 1,2 µl/min es en valores absolutos similar a la diferencia relativa de carga de buche para ese flujo (Fig. 3). Ello sugiere que ambas manifestaciones estan bajo el control de un mismo sistema. Las diferencias señaladas permitirían a la abeja A :

– mantener una comunicación más frecuente con la colmena y gracias a ello aumentar la eficiencia a nivel de la colmena al explotar el mercado de mayor diversidad del biótopo tropical en relación con el templado (Richards, 1973).

– obtener mayor flujo recolector dentro de una misma fuente floral gracias a una mayor velocidad recolectora.

Una disminución del tiempo necesario para comunicar una novedad a la colmena permitiría que el sistema que regula el reclutamiento tuviera mayor amplificación (Küpfmüller y Poklekowski, 1956). Sería dado esperar entonces que la amplificación de la respuesta de reclutamiento fuera mayor en las abejas A que en las E. En este sentido puede interpretarse la diferencia de respuesta entre las abejas A y E a un aumento transitorio del flujo en el simulador (Fig. 6a y 6b). La abeja A responde abreviando aún más la visita y como resultado recolectando menos y reduciendo aún más su eficiencia como recolectora con la posibilidad de comunicar anticipadamente la novedad en la colmena. En experimentos realizados con recolectoras de agua se ha observado algo equivalente. Luego de un estímulo térmico la respuesta de las A es más amplificada que la de las E (Núñez, 1979b).

Es un hecho aceptado y avalado por numerosas observaciones que un biótopo tropical es más rico en especies que un biótopo templado y que en este último la menor diversidad se compensa por una mayor abundancia de individuos de la misma especie (Richards, 1973). Ello ocurre también con las flores que ofrecen mayor monotonia en ambiente templado y concuerda con el hecho de que las abejas tropicales son polilécticas, es decir, durante la actividad recolectora cambian frecuentemente de especie explotada. Frente a esta mayor diversidad en las fuentes de alimentación la abeja africanizada presentaría mejor adaptación al disponer de un canal de información que le permite transmitir mayor frecuencia de cambios en las fuentes de alimento como puede esperarse de una flora variada. En una situación de mejor oferta transitoria, una mayor capacidad informacional como la que posee la abeja A puede resultar en una eficiencia recolectora muy superior (Núñez, 1977) al conseguir la prioridad en la explotación a expensas de otra línea (abeja E) que no posea estas características.

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ECOLOGICAL IMPACT OF AFRICANIZED HONEYBEES ON NATIVE NEOTROPICAL POLLINATORS

D.W. ROUBIK

Smithsonian Tropical Research Institute
APDO 2072 Balboa, Panamá

SUMMARY

A significant effect of the Africanized honeybee in the Americas is its interaction with resident pollinators. In French Guiana, Africanized honeybees nonaggressively displaced native highly-social bees from floral resources and artifical nectar sources. Compared to native *Melipona* and *Trigona* (Apidae : Meliponinae), Africanized honeybees may succeed in competition for floral resources due to 1) larger colony size ; 2) a more effective recruitment system ; 3) large individual size, and 4) impunity toward aggressive species of *Trigona.*

Experimental community studies in which the density of Africanized honeybee colonies was manipulated show that 10 to 15 colonies of 6,000 to 20,000 honeybees did not affect brood production, resource harvest or worker life spans of *Melipona favosa* or *M. fulva.* However, the experiment incorporated less than one tenth the number of honeybees colonies that might occur normally within foraging range of these social bees. Africanized honeybees were most similar in floral preference to *Melipona*, small anthophorids, megachilids, halictids and *Trigona.* These data are suggestive as to the *type* of bee Africanized honeybees might compete with most often. But without detailed information on the importance of a diet item to reproductive fitness, predictions regarding the population trends of particular bee species due to competition with Africanized honeybees cannot be made with precision.

RESUMEN

Impacto ecológico de las abejas africanizadas sobre polinizadores neotropicales nativos

Un efecto significativo de la abeja africanizada en las américas es su interacción con polinizadores nativos. En Guyana Francesa, abejas africanizadas desplazaron sin agresividad

abejas nativas altamente sociales desde recursos florales y alimentadores artificiales. En comparación con *Melipona* y *Trigona* indígenas (Apidae : Meliponinae), abejas africanizadas pueden competir exitosamente debido a 1) mayor tamaño de la colonia ; 2) un sistema de comunicación más eficaz ; 3) gran tamaño individual, y 4) impunidad hacia especies agresivas de *Trigona*.

Estudios experimentales a nivel de la comunidad ecológica, en los cuales se manipuló la densidad de colonias de la abeja africanizada, demostraron que 10 a 15 colonias de 6,000 à 20,000 abejas no afectaron la producción de crías, cosecha de polen y néctar, o duración de vida de obreras de *Melipona favosa* y *M. fulva*. Sin embargo, en los experimentos se empleó menos que una décima parte del número de colonias de abejas africanizadas que normalmente pudieran encontrarse dentro del rango de vuelo de estas abejas sociales. La abeja africanizada fué más similar en su preferencia floral a *Melipona*, anthophoridos pequeños, megachílidos, halíctidos y *Trigona*. Estos datos son informativos en cuanto al *tipo* de abeja con que la abeja africanizada puede competir con más frequencia. Pero sin información detallada sobre la importancia de un alimento en el éxito reproductivo de una especie, no se puede hacer con exactitud predicciones sobre el dinamismo de población que se espera en un polinizador particular debido a competencia con la abeja africanizada.

INTRODUCTION

Colonization of the American tropics by a hybrid of African and European *Apis mellifera*, the Africanized honeybee, has been viewed almost exclusively as a phenomenon influencing the beekeeping industry and public safety. These valid concerns are nevertheless a small subset of total interactions between an invading species and native plants and animals. Given that Africanized honeybees establish nests in many habitats (Brian, 1965 ; Michener, 1975 ; Roubik, 1979a) and reproduce continuously (Otis, this symposium ; Winston, 1979), widespread interactions with native neotropical plants and pollinators are inevitable (Roubik, 1978 ; 1979b, c ; 1980a). In this paper I consider the question of ecological impact on the most numerous and important group of neotropical pollinators : the bees.

My study took place in the lowland forest and savanna of French Guiana, an area that has never possessed feral populations of European honeybees nor been altered extensively by human activity. Africanized honeybees arrived in 1974 and were present at very low density during this study (Taylor, 1977). A unique characteristic of the region is its rich assemblage of highly social bees (Apidae : Meliponinae). In my study area alone there were 51 such species (Roubik, 1980b). In order to predict the course

of changes initiated by the invasion of Africanized honeybees in general, I pose the following questions, to be resolved in the remainder of the paper : How does the presence of the Africanized honeybee affect other highly social species through competition for food ? With which groups of bees is the Africanized honeybee most likely to compete ?

METHODS AND MATERIALS

All studies were made on a transect of lowland forest near Kourou, French Guiana (5°N). The area is primarily coastal forest and savanna having white, sandy soil, which is replaced some 14 km inland by continuous forest and red, lateritic soil. The details in methodology for each of my studies have been given elsewhere and thus are referenced in the following descriptions. The studies were initiated in July 1976 and terminated in August 1977. Three experimental studies were made to determine whether Africanized honeybees influenced 1) the abundance of native foragers within patches of flowers ; 2) foraging success of native bees at artificial resources which caused maximum recruitment of highly-social species ; 3) brood production, honey and pollen storage, and worker lifespan in observation hives of meliponines. One descriptive study assessed to what degree Africanized honeybees shared floral resources with native species. The experimental studies were performed with hives of Africanized honeybees that were established by trapping swarms which colonized beewax-lined «swarm boxes» (Taylor and Otis, 1978). Colonies were transferred to standard 10-frame Langstroth hives or 6-frame plywood hives measuring 24 x 22 x 42 cm. I trapped swarms at savanna-forest edges between Cayenne and Sinnamary.

Competition within flower patches. Near four species of ground-level flowers, 2-10 hives of Africanized honeybees were introduced and later removed to determine whether a change in honeybee abundance at flowers caused reciprocal change in the abundance of native foragers (Roubik, 1978 ; 1979b). In study plots contained within larger patches of flowers, I counted the number of foragers of different species at regular intervals beginning at the time of floral anthesis. Behavioral interaction between foragers also were noted.

Competition at artificial baits. Sixty experiments of 65 min duration were performed using 4 feeders on which honey-water of measured quality and quantity was presented. The experiments were made at 9 sites. The largest-bodied local aggressive species of *Trigona*, *Melipona fulva*, and polybiine wasps, primarily of the genus *Stelopolybia*, were attracted to the baits. In each experiment, the number of foragers of each species was counted on a feeder every 5 min. The experiments continued at a locality until one species had clearly displaced others or species partitioned the feeders and appeared to stably coexist. Honey-

water bait of 25 % or 50 % sugar content was used in the experiments, and aggressive interactions between foragers were noted (Roubik, 1979b ; 1980). The studies were made at the end of the wet season, when minimal floral resources were present (see Roubik, in press).

Competition at the level of the colony. Hives of *Melipona fulva* and *Melipona favosa favosa* were maintained at two sites. Feral colonies of the bees were located and transferred intact, with total colony stores of honey and pollen, to specially designed observation hives (Roubik, 1979a, b and in press). At three-day intervals, colony readings were made to determine 1) rate of brood production, 2) colony stores of honey and pollen, and 3) the age of tagged workers. These observations were made for a period of up to six months preceeding the introduction of honeybee hives. Africanized honeybee hives containing 6,000 to 20,000 workers were introduced for one month at each site, while I continued colony readings of the meliponine bees. Ten to 15 colonies of honeybees were used in each experiment. Few or no additional colonies of Africanized honeybees were within the study area. The experimental introduction of honeybees took place at the end of the wet season, in May and June.

Bee and flower associations. Collections of bees at flowers were made at all accessible species of flowering plants near Kourou for a period of 12 months. I tried to collect foragers or record their visitation at particular plant species in several localities and over a period of several days, until no new flower-visiting species were observed. The plants for which data were taken included 53 tree species, 44 shrub species, 24 species of vines and woody lianas, 21 species of sedges and grasses, and 56 additional species of herbaceous plants (Roubik, 1979b, c). Observations were made throughout the day and records were kept of foraging for pollen and/or nectar for each bee.

RESULTS AND DISCUSSION

Experimental studies

Forager abundance on *Borreria* spp. (Rubiaceae), *Mimosa pudica* (Fabaceae), *Rhynchospora globosa* (Cyperaceae) and *Melochia villosa* (Sterculiaceae) during experimental introduction and removal of Africanized honeybee colonies is given in Table I. Only in the experiments with *Melochia* and *Borreria* were there significant changes in the abundance of native foragers that coincided with experimental manipulation of honeybee colonies. At *Borreria*, however, no significant change in the abundance of Africanized honeybees at flowers took place. This experiment was the shortest of the series, and the changes in abundance that were recorded may have been spurious.

Observations were made for two days with the introduced honeybees present and two days in their absence. The change in native forager abundance was not related to the abundance of honeybees. In contrast, at the study plots of *Melochia*, increased abundance of honeybees corresponded with diminished abundance of highly social native bees (*Trigona c. cilipes* and *Melipona fulva*) at flowers. These species were more abundant when honeybee colonies were removed. Competition for floral resources is demontrated by these reciprocal changes. The experiments at *Melochia* lasted 12 days and included two separate 3-day introductions and removals of honeybee colonies. The probability that the reciprocal shifts in abundance were due to chance is 0.012 (probability of an observed increase, decrease, or absence of change in forager abundance = 1/3, therefore two reciprocal changes in forager abundance would occur with a probability of $(1/3^4)$.

Table I – F ratios for mean daily forager number during the presence of and after removal of Africanized honeybee hives. A nested two-level analysis of variance of forager numbers was performed for three forager classes. Nested groups of days were compared in which introduced hives of Africanized honeybees were present or absent. Subgroups within each group were censusing times. Degrees of freedom are : *Mimosa* (1,12), *Rhynchospora* (1,18), *Melochia* (1,8), and *Borreria* (1,12).

Tabla I – La razón F por el promedio del número de pecoreadoras diarias antes y después de remover colmenas de abejas africanizadas. Se realizó un analisis anidado de varianza de dos niveles del número de pecoreadoras para 3 clases de pecoreadoras. Se compararon grupos de días anidados, en los cuales colmenas de abejas africanizadas introducidas estuvieron presentes o ausentes. Los subgrupos dentro de cada grupo representan los tiempos de censaje. Los grados de libertad son : *Mimosa* (1,12), *Rhynchospora* (1,18), *Melochia* (1,8), y *Borreria* (1,12).

	Floral resource			
Forager class	*Mimosa**	*Rhynchospora*	*Melochia*	*Borreria*
Africanized honeybees				
During	9.6	81.5	111.3	371.0
After	0.0	7.5	72.0	365.0
F ratio	25.78^{+}	27.89^{+}	8.11^{+}_{+}	0.05
Stingless bees				
During	25.3^{β} 32.0^{λ}	65.6	23.3	124.5
After	19.1^{β} 44.5^{λ}	100.0	61.0	189.5
F ratio	2.10^{β}	1.08	6.80^{+}_{+}	14.5^{+}
Other native foragers				
During			51.8	22.5
After	not present	not present	60.1	59.0
			2.32	11.89^{+}

* Bees per 100 flowers. + P < .001. $^{+}_{+}$ P < .05. *Mimosa* : *Melipona fluva* and *M. favosa favosa* ; *Rhynchospora* : *Trigona (Tetragona) claviques* ; *Melochia* : *M. fulva* and *T. (Trigona) cilipes* ; *Borreria* : *M. fulva*, *M. favosa favosa*, and *T. (Trigona) cilipes* ; β *Melipona fulva* ; λ *Melipona favosa favosa*.

The Africanized honeybees did not interfere aggressively with other foraging insects, thus competition at *Melochia* appears to have been the result of declining food rewards perceived by native bees. The possibility of interference due to odors from the honeybees cannot be excluded as a subtle additional interaction which occurred during the experiments. Despite significant change in the rate of floral visitation by native bees on *Mimosa* after the removal of honeybee colonies, and the large amount of pollen that was collected by the introduced honeybee colonies at *Rhynchospora* (Roubik, 1978), the abundance of native bees did not change at these resources. Competition at these species might have been evident if total colony resource harvest had been measured for the social bees visiting the study plots.

The experiments at artifical feeders are discussed at length in another paper (Roubik, 1980a) and here I present the general results. Combined results from 37 experiments in which Africanized honeybees and native social foragers visited the feeders together are given in Fig. 1. Eighteen of the experiments included a single, small honeybee colony (5,000 - 8,000 workers) and 19 included 2 - 7 colonies. Eight species of *Trigona, Melipona fulva* and several wasp species foraged during these experiments. Honeybees dominated the feeders, particularly when the maximum amount of resource was applied to feeders (Fig. 1). The honeybees were not aggressive toward other species and did not abandon feeders readily when attacked by *Trigona*.

The largest, consistently aggressive *Trigona* eventually abandoned feeders visited by a large colony or several small colonies of Africanized honeybees. These *Trigona* were relatively inflexible in their aggressiveness, and they all but ceased to visit feeders at which they had arrived previously in large numbers. Such behavior is best explained as the result of a foraging cost (constant attack of numerous honeybees) that exceeded the gain (caloric reward of honey-water). Aggressive workers from single colonies of *T. hyalinata branneri* and *T. p. pallens (= T. pallida)* successfully displaced from feeders the honeybees of single, small colonies at two sites. In each instance of interspecific displacement, foragers from a displaced colony occasionally arrived at feeders and foraged successfully, but the response of the colony and the arrival of foragers that had been trained to visit the feeders declined abruptly. This change in response never occurred at relatively uncontested feeders.

Colonies of *T. h. branneri* and Africanized honeybees were far larger than those of the other species. The size of a mature honeybee colony is 10-100 times that known for the *Melipona* and as much as 10 times larger than most *Trigona* colonies (Michener, 1974 ; Roubik, 1979a, 1980a and in press). In addition, no highly social bee except *Apis* is able to recruit many nest mates to a resource in a short time, without the necessity of providing

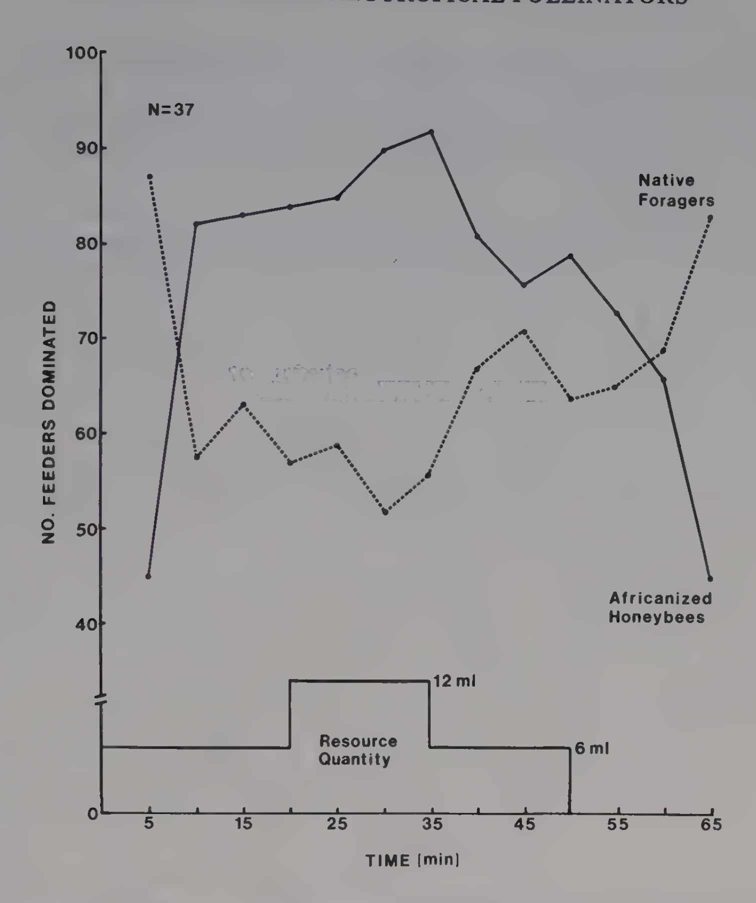


Fig. 1 – Dominance of individual feeders (numerical superiority) by Africanized honeybees or combined native foragers. The data are from 37 experiments, each incorporating 4 feeders ; 13 counts of foragers were made at each feeder in a 65-minute experiment. «Resource Quantity» is the amount of bait applied to a feeder at 5-minute interval.

Fig. 1 – Dominancia (superioridad numérica) de abejas africanizadas o combinación de pecoreadoras nativas sobre alimentadores individuales. Los datos son de 37 experimentos, cada uno incluyendo 4 alimentadores ; se hicieron 13 conteos de pecoreadoras por cada alimentador en un experimento de 65 minutos. «Cantidad de Recurso» es la cantidad de cebo aplicada a cada alimentador a intervalos de 5 minutos.

odor trails or guiding other foragers (Michener, 1974). The relatively large size of *A. mellifera* implies a larger flight range than the *Trigona* and a foraging range comparable to *Melipona* (see Eickwort and Ginsberg, 1980 ; Michener, 1974 ; Roubik, 1979c). The large colony size, more precise recruitment system, particularly for long distances (von Frisch, 1967), and impunity toward aggressive *Trigona* provide Africanized honeybees with a competitive

advantage over stingless bees in locating and exploiting rich resources. Other factors being equal (sensitivity to floral odors and response to meteorological conditions, for example), a large colony or multiple colonies of Africanized honeybees should be able to dominate many of the floral resources used by neotropical social bees.

Demonstration of competitive superiority at a particular place or time need not imply that an introduced species will displace another from a geographic area. Particularly for highly social bees which exploit a large proportion of the available flowering plants (Percival, 1974 ; Sakagami, Laroca and Moure, 1967 ; Johnson, 1974 ; Heithaus, 1979 ; Roubik, 1979a, b ; Absy and Kerr, 1977), diminished foraging returns or even total displacement at a resource need not lead to substantial loss at the level of the colony. To test whether probable competition among such generalist foragers affected the functioning of the colony, my introduction-removal experiments were designed to test the null hypothesis that no significant changes occurred in intracolony processes of meliponine bees as a result of the number of Africanized honeybees in close proximity. Acceptance of the null hypothesis does not signify the absence of competition at all levels, but only that intense competition did not accur.

Analysis of data collected as time series presents special statistical problems (Box et al., 1978). One means of circumventing such problems is the technique of repeated-measures ANOVA (Winer, 1971). This method was applied to data from 5 meliponine bee colonies to test for a change in intracolony parameters during three experimental treatments : the absence of honeybee colonies, introduction of honeybee colonies and removal of honeybee colonies. The result are presented in Table II. The statistical model of repeated measures ANOVA predicates independence between subjects (bee colonies) and is applied to analyze the effect of a treatment on subjects that were monitored simultaneously (Winer, 1971). Further, I analized the rate of change of intracolony parameters (the differences between successive readings) rather than the raw data series. No «control» colonies were used in the experiments because a suitable number of colonies in the same stage of their colony cycle (Oster and Wilson, 1978) was not available.

No change in the amount of stored honey, pollen or newly constructed brood cells occurred due to the change in number of introduced Africanized honeybee colonies (Table II). Meliponine worker life spans increased during the period of honeybee introduction, but this was a seasonal trend due to floral scarcity not related to competition with the honeybees (Roubik, 1979b and in press).

The 30-day period in which honeybees were introduced at each site coincided with the end of the wet season and a floral dearth period.

Table II – Results of repeated measures analysis of variance of the rate of change in intracolony parameters that coincided with three experimental treatments of differing honeybee colony density (see text).

Tabla II – Resultados del análisis de varianza de medidas repetidas de velocidad de cambio de los parámetros intracoloniales que coincidieron con tres tratamientos experimentales de diferentes densidades de colonias de abejas melíferas.

Colonies observed (number)	Intracolony variable	Treatment means *			df	F	P
		before	during	after			
M. favosa (2)	honey	-4.14	-1.61		1,2	2.61	0.25
M. fulva (1)	pollen	-0.09	0.01		1,2	1.80	0.31
	brood	-0.14	0.10		1,2	0.13	0.76
M. favosa (1)	honey	-5.30	-2.34	-1.00	2,2	2.81	0.26
M. fulva (1)	pollen	-0.13	-0.02	0.01	2,2	0.69	0.59
	brood	-0.21	-0.13	-0.13	2,2	0.05	0.97

* Means for honey and pollen are in cm^3 ; brood is expressed in the average number added to the colony per day. The data are presented as rate of change, i.e. differences between successive observations.

The colonies of *Melipona* were experiencing a seasonal decline in brood production and colony stores (Table II). Nevertheless, they brought food to the nest, as did the introduced honeybees (Roubik, 1979b). A lack of intense competition could have been due to the use of different resources during this period. However, of the 75 known floral resources used by *M. fulva* during the year of my study, and the 26 used by *M. favosa*, at least 50 % also were used by honeybees (Roubik, 1979b and in press, see also Table III). It seems that competition may have occurred, but at levels too low to be detected within the nest. Furthermore, the 10-15 colonies of Africanized honeybees used in the experiments were probably the only colonies within the foraging range of the *Melipona*. In a naturally colonized habitat, the density of Africanized honeybee colonies has been estimated at 10 colonies/km^2 to 107 colonies/km^2 (O. Taylor, personal communication and Kerr et al. in Michener, 1975). The foraging range of *Apis mellifera* is at most 14 km (Eickwort and Ginsberg, 1980) and a foraging range of 5 km is common (Gary et al., 1977 ; N.E. Gary, personal communication). The demonstrated foraging range of *Melipona* is at least 2 km (Wille, 1976 ; Roubik, unpublished data). Combining this information, an individual colony of *Melipona* potentially competes with honeybee colonies within a 7 km radius. At Africanized honeybee colony density of 1/km^2, a *Melipona* colony may compete with the foragers of 154 honeybee colonies. Competition is therefore potentially far more intense between Africanized honeybees and native *Melipona* than that which was possible in the present study.

Table III – Floral resource use and diet overlap among Africanized *Apis* and neotropical bees.

Tabla III – Uso de recursos florales y sobreposición de dietas entre *Apis* africanizadas y abejas neotropicales.

Bee genus	*An*	*Ap*	*Aa*	*Ao*	*Bo*	*Cn*	*Cr*	*Ep*	*Eg*	*El*	*Fl*	*Mg*	*Ml*	*Ms*	*Tt*	*Tr*	*Xy*
No. bee species	3	1	12	6	1	25	10	6	25	6	1	14	7	1	18	37	12
No. floral resources	14	75	34	26	20	38	17	11	38	14	12	36	79	15	23	165	63
Diet overlap with *Apis*	.71	1.00	.62	.46	.05	.18	.65	.18	.21	.00	.83	.61	.50	.73	.43	.32	.29

An : *Anthidiinae*
Aa : *Augochlora*
Ao : *Augochloropsis*
Ap : *Apis*
Bo : *Bombus*
Cn : *Centris*
Cr : *Ceratina*
Ep : *Epicharis*
Eg : *Euglossa*
El : *Eulaema*
Fl : *Florilegus*
Mg : *Megachilde*
Ml : *Melipona*
Ms : *Melissodes*
Tt : *Paratetrapedia* + *Tetrapedia*
Tr : *Trigona*
Xy : *Xylocopa*

Resource use

Resource use by coexisting species is a central topic of population and community ecology. The implictions of observed resource partitioning among species are seldom clarified (Schoener, 1974 ; Wiens and Rotenberry, 1979 ; Hutchinson, 1979), but the situation is somewhat more straightforward when a colonizing species is involved. Conventional ecology emphasizes overlap of resource use in space and time and the effect that the rate of food harvest by one species has on the reproductive fitness of other species using the same resource (Hutchinson, 1979). It is often tacitly assumed that the number of diet items held in common between species directly influences the degree to which they compete (Cody, 1974 ; Pianka, 1976 ; Percival, 1974 ; Moldenke, 1975 ; Heithaus, 1979). But this is true only if all diet items are equally important to reproductive fitness. The data presented in Table III should be interpreted accordingly. At the least, they indicate which groups of bees might compete most often with the Africanized honeybee and which would seem not to compete frequently, relaitve to their recorded floral preferences.

With the exception of Africanized *Apis mellifera*, I combined the data on floral preferences of bees of closely-related species. Of the 37 bee genera included in my study (Roubik, 1979b, c), what seem to be adequate or representative data were available only for the 17 genera listed in Table III. A graphic representation of the similarity in resource use among these genera is presented in figure 2, the result of principal component analysis (see Harris, 1975 ; Poole, 1974). A possible shortcoming of the resource data is that only a moderate percentage of the total resources used by bees could be included. Further, the implicit assumption in the analysis is that the species of a particular genus are more similar to congeners in resource use than they are to species of other genera. This assumption may be false in some instances (Heithaus, 1979). However, the data include a broad variety of flowering plants (see Methods and Materials, also Roubik, 1979b, c), and thus may adequately represent this plant-pollinator community. It seems reasonable that closely related species share structural and behavioral attributes that determine which resources they are able to use (Michener, 1979 ; Michener, et al., 1978 ; Inouye, 1978 ; Thorp, 1979). Therefore, the lumping of congeners for the purpose of understanding resource use patterns may be justified. Moreover, the information gathered during one year of observation does not seem to warrant comparative studies of resource use among individual species (see Wiens and Rotenberry, 1979).

The most striking pattern emerging from the data given in Table III and Fig. 2 is that Africanized honeybees share a large proportion of the resources

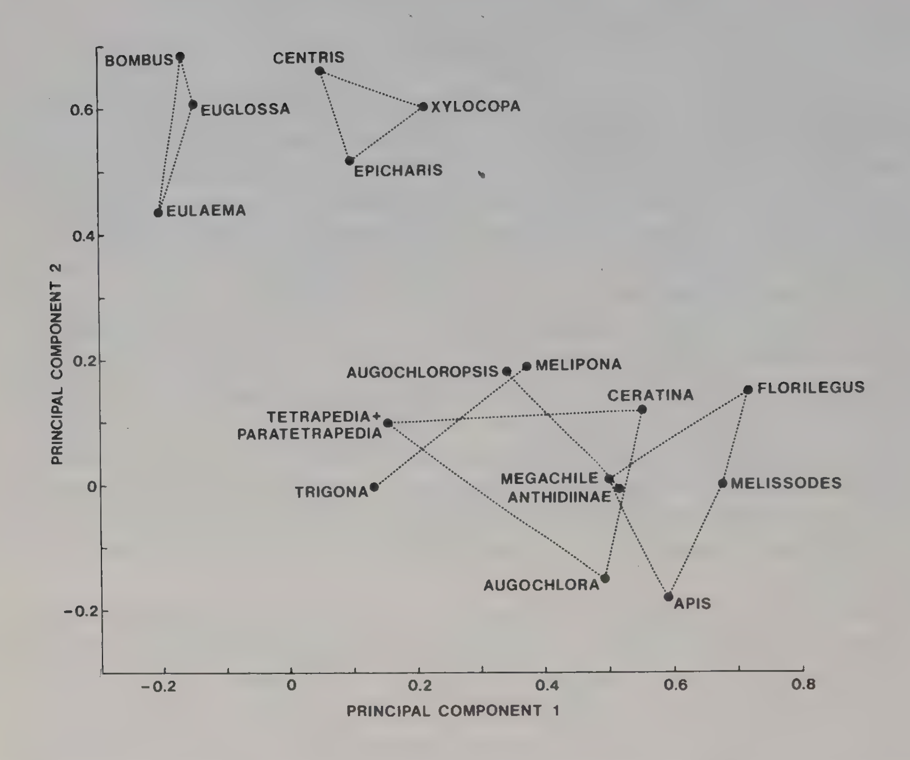


Fig. 2 – Similarity in floral resource use among Africanized honeybees and 17 neotropical bee genera, presented on two axes specified by a principal component analysis. The dashed lines connect genera that clustered together on rotated principal axes which accounted for 51 % of the observed variance in floral preference among bee genera.

Fig. 2 – Similitud en el uso de recursos florales entre abejas africanizadas y 17 géneros de abeja neotropicales, presentados en dos ejes especificados por análisis de componente principal. Las líneas entrecortadas conectan géneros que se agruparon en ejes principales rotados y que explicaron el 51 % de la varianza en preferencia floral entre géneros de abejas.

used by medium-sized to small bees, and not many with the larger bees. Similar associations have been seen among European honeybees and native bees in Costa Rica dry forest (Heithaus, 1979). In French Guiana, bees visiting a species of flower almost always collected nectar and pollen when both were available. Yet it is possible that these resources, although from a single species of flower, may represent different contributions to the fitness of bees. Oligoleictic species, bees that restrict their pollen use to a small number of species, probably sustain greater reproductive loss due to competition for pollen with Africanized honeybees than do other species. The limited available data suggest that many species of small anthophorids and

megachilids tend toward oligoleicty in the tropics (Heithaus, 1979 ; Roubik, 1979b, c and Table III), although these species are seldom restricted to one or two species of pollen, as are oligoleictic species in temperate areas (Raw, 1976 ; Michener, 1979). The more generalized flower visitors such as meliponine bees may be less dependent on a small number of resources and thereby less susceptible to competition with generalist honeybees. Even if native species are more efficient at exploiting a particular flower (see Strickler, 1979) than are Africanized honeybees, the sheer numbers of Africanized honeybees arriving at a flower patch from an individual colony plausibly alters their efficiency both through incidental interference (Roubik, 1980a) and depletion of floral rewards. Considering both generalist and specialist bees in the tropics, competition for flowers must be assessed ultimately in terms of reproductive fitness. At present, a crucial question for future research can be phrased : how important is a species of flower to the reproductive fitness of its visitor ? I suggest that this question has not been answered for any tropical apoid.

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BEHAVIORAL GENETIC ANALYSIS OF COLONY-DEFENSE BY HONEY BEES*

T.E. RINDERER

Bee Breeding & Stock Center Laboratory,
AR, SEA, USDA, Baton Rouge, Louisiana 70808, U.S.A.

SUMMARY

Defensive behavior in honey bees is a complicated behavioral sequence of actions. The sequence includes four major categories : alerting, activating, attracting, and culminating. Each major category has sub-categories of possible responses. Because of this, complex variation exists among the colonies. Surveys of the defensive behavior of European and Africanized bees showed that in time-limited tests, Africanized bees were ca. 10-fold more defensive than European bees. Measurements of hybrids showed that most genes which intensify defensive behavior are dominant.

RESUMEN

Análisis genético de la conducta defensiva de las colonia de abejas

La conducta defensiva de las abejas es el resultado de una complicada secuencia de actividades interconectadas. Tal secuencia la conforman 4 importantes tipos de actividad : alerta, activación, atracción y culminación, cada una de las cuales esta compuesta por sub-actividades o respuestas posibles que son ampliamente variables entre colonias. Pruebas de conducta defensiva demostraron que, en ensayos de tiempo limitado, las abejas Africanizadas tienen una conducta defensiva diez veces superior a la de las Europeas. Los resultados de las mediciones realizadas en los híbridos, mostraron que la mayoria de los genes responsables del aumento del comportamiento defensivo son dominantes.

* In cooperation with the Louisiana Agricultural Experiment Station

The two scholarly reviews of African- and Africanized-bee literature both give considerable attention to the readiness and capability of these bees to defend their colonies (Fletcher, 1978 ; Michener, 1975). This attention is certainly not unfounded. The sight of a colony of Africanized bees engaged in a massive defensive response commands the undivided attention of an observer, and reports of such events have made vigorous colony defense the best known characteristic of Africanized bees. Since Africanized bees are so capable of defending their colonies, considerable efforts have gone to the study of their defensive behavior. One hope spurring these studies is that modification through selective breeding can help dampen the intensity of this behavior and thereby reduce at least some of the problems caused when a bee population becomes Africanized. However, successful modification of defensive behavior by selective breeding will rest on a reasonable understanding of the genetic elements that regulate this behavior.

Before fruitful genetic experiments themselves can be undertaken, defensive behavior itself must be reasonably well understood. To be most useful, this understanding must include three elements. First, the individual activities which together comprise this complex behavior must be identified. Second, techniques must be devised to measure qualitatively or, as appropriate, measure quantitatively the activities comprising the behavior. Third, sufficient surveys of bee populations must be made to verify that at least some of the component activities as measured by the devised techniques are both adequately consistent in single colonies of bees and also differ between colonies.

The identification of the individual activities comprising colony defensive behavior is not a small task. Even a cursory review of work published on defensive behavior in honey bees reveals that almost every worker in the field has studied a somewhat different aspect. Some researchers have studied the non-stinging alert response to alarm pheromones by bees in field colonies (Boch et al., 1962, 1970 ; Ghent and Gary, 1962 ; Maschwitz, 1964, 1966 ; Shearer and Boch, 1965), and others have studied this same response by bees in small laboratory cages (Collins and Rothenbuhler, 1978). Still others have explored the ability of a variety of stimuli such as color, odor, and movement to elicit stinging by bees (Free, 1961 ; Free and Simpson, 1968 ; Koeniger, 1978). Beyond these basically qualitative studies, several attempts to quantitatively measure non-stinging features of colony defense (Boch and Rothenbuhler, 1974) and also specific aspects of stinging have been made (Gonçalves and Stort, 1978 and Stort, 1970, 1974, 1975a, 1975b, 1975c, 1976). The variety of response measured in these different studies indicates that colony-defensive behavior is a complicated collection of actions. Indeed, when attempting to understand this behavior from a synthesis of published

research and personal observation, the paramount emergent conclusion is that the defense behavior of honey bees is extremely diverse and complex.

In an attempt to provide some order to this diversity and complexity, a classification model of defensive behavior has been developed (Collins et al., 1980). This model recognizes two central features of colony defense. First, many actions are clearly temporally sequential. In light of this, the model identifies four discrete sequential steps within the full behavior : alerting, activating, attracting, and culminating. The second central feature of defensive behavior recognized by the model is that at least in the alerting and culminating steps several possible actions may occur which are mutally exclusive, at least temporally. Some bees may, in time, perform all these actions but probably this is not the case for most bees.

The four major steps are reasonably straightforward. In the alerting step a bee may assume a characteristic alert posture (Ghent and Gary, 1962), may recruit other bees by running into the hive with her sting chamber open and her sting protracted (Maschwitz, 1964) or may simply withdraw into the hive. After responding in any of these three ways a bee may then become activated. If activated, a bee seeks the source of disturbance. This search, if the source is not found, may extend to several meters from the hive. In fact, I have observed activated Africanized bees a measured 120 M from their colony. Once an appropriate stimulus source is found a bee orients or is attracted to that stimulus. After having drawn near the source of the disturbance the bee may engage in a culminating response or a sequence of such responses. Among these responses the model identifies threat actions, during which the source of stimuli is not touched. Also identified are burrowing, biting, hair pulling (which is perhaps a variant of biting), and stinging ; all of these actions involve contact with the stimulus source. To this list I add head-bumping. In recent experiences with Africanized bees I observed that on several separate occasions bees in flight repeatedly and forcefully bumped their heads into the stimulus source. In one instance I counted 17 such bumps before the bee finally stung. Lastly, the option of leaving the vicinity of the disturbance is given by the model.

This model supplies an organized classification of the complicated collection of actions which together comprise defensive behavior. It thus permits the development of a system of testing and measurement which is designed to show defensive responses in a clear systematized fashion. Such a measurement system has been developed by staff at my laboratory. Generally, a variety of stimuli are presented to a colony of bees in such a way that the steps in the process of defense can each be observed and measured. Since many responses are momentary, portions of the data are initially recorded on film or videotape.

As yet unpublished experiments evaluating the testing system showed that the data it produces are quite satisfactory. The four major steps of the model were both apparent and measured. Also, repeated tests of the same colony gave essentially the same results. Using this measurement system, surveys have been made of the defensive behavior of approximately 150 colonies of European bees in Louisiana and 150 colonies of Africanized bees in Venezuela. These surveys showed no qualitative but strong quantitative differences between bees in the two populations. At all steps in the defensive process, Africanized bees responded much more quickly to stimuli. For example, when given stimuli appropriate for cueing culmination, Africanized bees responded 33 times more quickly than European bees. Our testing procedure provides an opportunity for bees to sting an object for a period of 30 seconds. Africanized bees stung 8.5 times more than European bees during this period. Generally, when considering the entire test sequence, Africanized bees proved to be ca. 10-fold more defensive than European bees.

These surveys were accompanied by a more closely controlled experiment using small Africanized and European colonies of identical sizes in Venezuela. This comparison revealed differences between European and Africanized bees of similar magnitude and direction to those found in the survey.

As well as providing evidence for the rather obvious conclusion that Africanized bees deserve their reputation as able colony-defenders, the survey also provided two important pieces of information. First, and most importantly, the magnitude of the difference between the defensive responses of populations of Africanized and European bees has been quantitatively documented. Heretofore, such differences have been reported qualitatively or as numerical differences between a few selected colonies. Second, strong differences were not only shown to exist between European and Africanized populations of bees but also between colonies of similar racial origin. These observations strongly support the notion that breeding programs designed to produce less defensive Africanized bees stand a good chance of success.

With a working model of defensive behavior, an adequate system of measurement and the assurance that measurable differences occur between the responses of different colonies of bees, a wide variety of genetic experiments can be conducted. The first and rather obvious experiments are to evaluate the defensive responses of hybrid bees resulting from crosses of colonies that differ strongly. We have done several such experiments both within and between European and Africanized bees. The results of these experiments indicate that F_1 hybrids generally tend to show defensive behavior similar to or, in certain cases, greater than the more defensive parent. Generally, for each step in the sequence of colony defense, these experiments indicate that most genes which intensify defensive behavior are dominant.

Thus Africanized-European hybrids defend their colonies very much like their Africanized parents. Thus far, the results of our experiments suggest that the production of less defensive stocks of bees will be done through careful and rather slow selection programs. There is one notable exception. One specific F_1 hybrid we tested repeatedly followed the general trend of F_1 hybrids for the steps of alerting, activating, and attracting. That is, they were quick to become alert, intensively recruited other bees to defense, and quickly searched out a source of disturbance. However, at that point they went no further. They simply flew near the source of disturbance, but did not sting it nor did they engage in any form of culmination activity. Thus, there is the possibility that, although somewhat rare, important genes exist which tend to strongly reduce the intensity of defensive behavior. The early incorporation of such genes into stocks of bees would speed the progress of selection programs designed to produce tractable bees.

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EFFECTS OF BRAZILIAN CLIMATIC CONDITIONS UPON THE AGGRESSIVENESS OF AFRICANIZED COLONIES OF HONEYBEES

M.M. BRANDEBURGO[1], L.S. GONÇALVES[2], W.E. KERR[3]

Departamento de Genética – Faculdade de Medicina de Ribeirao Preto
Universidade de Sao Paulo – 14.100 Ribeirao Preto SP, Brazil

SUMMARY

The present research is related to a study of the effect of climatic conditions upon the aggressiveness of Africanized bees in two different regions of Brazil, Recife in the Northeast and Ribeirão Preto in the Southeast. The study was based on a program of successive queen transfers and on aggressiveness tests, carried out after each queen transfer. Five behavioral and two climate variables were studied, as well as the weight of the hive as a control on population size. This research was carried out from August 1975 to March 1977. The following main results and conclusions were reached :

a) The Africanized colonies (controls) in the Recife region were much more aggressive (three to fourteen times as much) than the Africanized bees (controls) in the Ribeirão Preto region.

b) The group of colonies derived from transferred queens (SP-queens and PE-queens) which were tested in both climatic regions, responded differently each time they were reconstituted after queen transfer from one region to the other. Thus, the pool of genes representative of the Africanized bees from each of the two Brazilian regions were submited to the climatic conditions of Ribeirão Preto and Recife throughout the whole experiment. The small differences observed between the averages of PE and SP colonies tested in both regions for the five behavioral characteristics were not statistically significant. The main responsibility for the different behavioral responses recorded in Ribeirão Preto and in Recife was atributed to climatic conditions.

c) Africanized colonies descended from both SP and PE queens showed the same aggressive response when tested in Ribeirão Preto ; likewise in Recife. The bees derived

from SP and PE transferred queens were much more aggressive in Recife than in Ribeirão Preto.

d) In general, supposing that the Africanized bees from each region studied are hybrids which are being selected in nature by the climatic conditions of each region, the results indicate that natural selection for aggressiveness was surprisingly almost the same for bees from both regions. The main responsibility for the different aggressive response of Africanized bees in Ribeirão Preto and in Recife is attributed to immediate effects of climatic conditions.

e) The temperature in Recife is at least 5°C higher than in Ribeirão Preto and much more stable. In Recife there is practically no winter season. The relative humidity in Recife is higher than in Ribeirão Preto and more stable. The precipitation in Ribeirão Preto is higher than in Recife and better distributed through the year.

f) There was a significant correlation among all the 5 variables related to aggressive behavior, which confirms the results of Stort (1971).

g) The temperature at the moment of the aggressiveness test had influence on the aggressive behavior of the Ribeirao Preto bees (positive correlation) and on the Recife bees (negative correlation). These results were different from those obtained by Stort (1971).

h) According to correlation analysis with total data, relative humidity has a significant influence on the aggressive behavior of bees. The analysis of data collected in Ribeirão Preto only, showed no significant correlation. The data collected in Recife showed a positive correlation between humidity and «Number of stings in the leather ball». Relative humidity in Recife is higher than in Ribeirão Preto and, considering that the Recife bees are much more aggressive (three to fourteen times as much) than the Ribeirão Preto ones, it can be concluded that humidity plays an important role as an external factor on the aggressive behavior of the bees.

RESUMEN

Efecto de las condiciones climáticas de Brasil sobre la agresividad de colonias de abejas africanizadas

El trabajo fué desarrollado en Ribeirão Preto-SP y Recife-PE, en Brasil, con la finalidad de comprobarse la influencia del clima en el comportamiento hostil de las abejas africanas. Fueron utilizadas 40 colmenas en cada lugar, siendo ellas pobladas con abejas africanizadas, obtenidas en las regiones de estudio (muestra SP y PE). Todas las colmenas tuvieron su hostilidad, esto es, comportamiento de defensa, probados según la prueba desarrollada por Stort (1974) y los resultados iniciales muestran que las abejas de Recife son cuatro veces más hostiles que las de Ribeirão Preto.

Después, fue ejecutado un plano de transposición de reinas de Recife para Ribeirão Preto y en sentido contrario, siendo luego las colmenas medidas nuevamente, después de

60 días. Este fué el tiempo necesario para que las obreras fueran substituidas por obreras hijas de las reinas transportadas. Los resultado mostraron que las abejas de ambas colmenas al ser trasladadas para Recife, eran mas hostiles, mientras que en Ribeirão Preto la hostilidad disminuyó.

El análisis de los resultados de hostilidad (defensa) muestra que la diferencia inicial de hostilidad entre las abejas fué debido a la diferente influencia del ambiente de las regiones de Recife y Ribeirão Preto, y no la diferencia entre las proprias abejas. Se notó también, que la diferencia de comportamiento hostil inicial se reduce con la permanencia de las abejas SP e PE en un mismo lugar.

El estudio de alguna relación entre los datos climatológicos y ambientales, muestra una relación positiva entre la humedad relativa y la hostilidad de la abeja, y relación negativa entre la variación de la temperatura y el comportamiento hostil.

De acuerdo a otros trabajos, es probable que la influencia de la humedad relativa no sea directa, y si, por intermedio de variaciones en el potencial electrostatico de la colmena.

Otros factores climatológicos como la temperatura, el estado general del tiempo y la lluvia, presentan relación con la hostilidad. Lo mismo sucede con el peso de las colmenas, aunque este factor se tenga relacionado negativamente con la lluvia, lo que puede ser de posible interés para el estudio de la biologia de la abeja africanizada.

También se observó, que al compararse los resultados obtenidos por Stort (1974) en 1965, con nuestros resultados en 1976, hubo una disminución en la hostilidad de las abejas africanizadas de la region de Ribeirão Preto, SP.

INTRODUCTION

Over the last ten years, increased attention has been focused on the problem of bee aggressiveness related to the introduction of African bee (*Apis mellifera adansonii*) into Brazil and their possible future spreading throughout the Americas. African bees were introduced into Brazil in 1956 in an attempt to increase honey production. Unfortunately, however, in 1957, 26 queens, mated in Africa, escaped with swarms from an experimental apiary near Rio Claro, SP. (Kerr, 1967). The drones from these swarms and the new queens mated with the European subspecies present in the surrounding areas with the resulting formation of hybrids. These hybrids are correctly called «Africanized bees» because they are not native and because they sometimes resemble *Apis mellifera adansonii* in several behavior characteristics, especially aggressiveness.

The spread of Africanized bees from 1956 to 1977 has been relatively rapid. The extent of the occupied area was described by Kerr (1968), Gonçalves (1974), Michener (1975) and Taylor (1977). According to

Taylor (1977), Africanized bees were found in Guyana and Venezuela in 1976. Several morphological and behavioral characteristics must be studied in order to recognize an Africanized colony of bees but unfortunately attention has been focused only on aggressiveness. This procedure has been causing much misinterpretation in the identification of these bees.

It must be remembered that the behavior of any strain of honeybees, as for instance aggressiveness (considered as a phenotype), is the product of interaction between the genetic composition of the individuals (genotype) and environmental factors. In many cases it is difficult to decide which of these components (genotype and environment) is the more important. Genetic analysis of behavior is only possible when there is homogeneity in the population which is being studied. This is only obtained through mating control, for instance with the use of artificial insemination, and with inbred lines.

The first evidence indicating genetic control of aggressive behavior of honeybees was that of Rothenbuhler (1960 ; 1964) who analyzed two inbred lines of honeybees (Van Scoy and Brown Lines) which were different in temperament. He showed that the difference in stinging behavior between the two lines was controlled by more than two loci. The differences in temperament between Italian and Africanized bees have been studied in detail by Stort since 1970, using methods to measure the aggressiveness of bees (Stort, 1970, 1971, and Gonçalves & Stort, 1977). Stort carried out several aggressiveness tests with Africanized and Italian parental colonies of bees, F_1-hybrids, as well as Africanized and Italian backcross colonies ; he concluded that eight is the number of genes involved in the aggressive behavior (Stort, 1971 ; Gonçalves & Stort, 1977). However, it is important to mention that the same genotypes can produce completely different behavior because of environmental influences. Many behavioral patterns in honeybees are caused primarily by external stimuli such as temperature, light, chemical products, humidity, etc., which are detected by a network of specialized sensory cells. The same genotype submitted to different environmental conditions such as different climates can produce completely opposite responses.

In honeybees, aggressiveness is caused primarily by internal factors (eight genes, according to Stort) but it is well known that this behavior is influenced also by external factors such as smoke, chemicals, smell, touch, sounds, etc. The genes for aggressive behavior interact with environmental factors to produce the final behavioral phenotype. Schua (1952) concluded that the aggressiveness of colonies increases with external temperature, a fact confirmed by Rothenbuhler (1974). However, Stort (1971), while working on the aggressiveness of Italian and Africanized backcrosses, not under the direct

incidence of the sun rays, did not confirm the influence of temperature, at least under the climatic conditions of Ribeirão Preto, São Paulo, Brazil. According to Lecomte (1963), the influence of wind and stormy weather on the aggressiveness of bees is important but the influence of temperature is less certain. Warnke (1976) reported that changes in weather and clouds produce local changes of electric charge on individual bees and in the colony, and this fact influences aggressive behavior. Other external factors, such as nectar flow, also influence honeybees' aggressiveness (Lecomte, 1963 ; De Santis & Cornejo, 1968). This report describes a study on the effects of Brazilian climatic conditions upon the aggressiveness of Africanized colonies of honeybees. The research was planned and carried out with the financial support of the United States Department of Agriculture and with a cooperative agreement between the USDA and the Departamento de Genética da Faculdade de Medicina de Ribeirão Preto, University of São Paulo.

Two sites for the aggressiveness tests were : the Southeast Experiment Station in Ribeirão Preto, São Paulo State, with an apiary located about 5 km from the Department of Genetics, and the Northeast Experimental Station, located in Recife, Pernambuco State, about 2500 km north of Ribeirão Preto, with the apiary located near the Tapacurá flood-gate, about 37 km from the Departamento de Zootecnia da Universidade Federal Rural de Pernambuco. The climatic conditions of both regions are given in Table III and Figures 5 and 6, and will be discussed later.

MATERIAL AND METHODS

Forty Langstroth hives were located in Ribeirão Preto and populated with honeybees collected in this region, and 40 were located in Recife and populated with Africanized bees from that region. Thus, each lot had bees with a gene pool representing the typical genotype of the region. Each hive was painted and numbered. The open mated queens were marked with colored plastic numbers, white for the queens from Ribeirão Preto (SP_1 to SP_{40}), and green for the queens from Recife (PE_1 to PE_{40}). Colonies in each apiary were housed two meters apart. In order to study the effect of the climatic conditions of each region upon the aggressiveness of the Africanized honeybees, the colonies were submitted to aggressiveness tests in order to select colonies whose queens should be transferred from one station to the other simultaneously. A group of 10 colonies was left in each apiary as control. The aggressiveness tests were done according to Stort's method (Stort, 1970, 1971), which consists basically of the following : small black leather ball stuffed with cotton, about three centimeters in diameter, is jerked up and down for 60 seconds at a distance of five centimeters from the entrance of the hive. After this time the observer leaves the place. In order to avoid disturbing the colonies being

tested, the hives were transported two at a time the night before the test, to a place about two km from the apiary by a roadside where the observer could walk at least two km, in order to record the distance of persecution by the bees. The following data were recorder :

– Time until the first sting to the leather ball.
– Time for the colony to become aggressive.
– Distance that the bees follow the observer.
– Number of stings in the leather ball.
– Number of stings in the gloves of the observer.
– Weight of each colony on the day of the test.
– Temperature at the moment of the test.
– Relative humidity of the region.

The aggressiveness test was repeated five times on each hive at 20 minute intervals, using a fresh leather ball each time. All the tests (four series) were done by the same observer (Brandeburgo), in both regions and at the same period of time. It took about 45 days to carry out each series of aggressiveness tests for all the hives of both stations. The first series of aggressiveness tests was made in August 1975 for the 40 colonies of each station. After the tests, the queens of 30 colonies from Ribeirão Preto were transferred to Recife and the queens of 30 colonies from Recife were brought to Ribeirão Preto. Ten colonies were left in each station as controls. The queens were transported by airplane in small cages with 8 to 10 workers. After the transfer, the queens were immediately introduced into the hives with the 2nd series of aggressiveness tests being carried out only 70 days later, and so on. This procedure is due the fact that the life span of the workers averages 45 days ; thus, all the bees found in the colonies would be offspring of the transported queen. The four series of tests were carried out at both stations (August-September 1975 ; February-March 1976 ; July-August 1976 ; January 1977). About 20 % of the queens were lost during each trip, either during transportation or at the time of their introduction into the hives. The lost queens were replaced with other queens and the same procedure repeated. After 70 days the offspring of the new queens was tested, and so on.

After the first queen transfer, 20 to 25 queens were brought back to their original station after the aggressiveness tests. The remaining 5 to 10 queens stayed at the new site. This meant that few Africanized colonies from the region of Ribeirão Preto stayed in Recife up to the end of the experiment, and vice versa. With this program of queen transfers, it was possible to submit the same genotype at two different seasons of the year to different environmental conditions, such as different temperature, humidity, precipitation, flora, etc. The influence of some of these external factors on the aggressive behavior of Africanized bees (phenotype) was studied.

To analyse the data collected in both regions on offspring of the transferred queens and the controls, we calculated the average of the five repetitions in each series of tests for each variable and for each colony. Finally, the averages of the behavioral characteristics of the Africanized bees of each region were estimated. The controls were analyzed

independently of the offspring of transferred queens. The averages of the Ribeirão Preto colonies were compared with the averages of the Recife colonies, for each variable studied (1st series of aggressiveness tests). After the first transfer, the data for both the transferred lots and the controls were compared. For instance, a comparison was made of the averages for the bees from Ribeirão Preto tested in Ribeirão Preto and later tested in Recife. These averages were compared also with the controls of both regions. The same was done with the bees from Recife which were brought to Ribeirão Preto. The same procedure was followed in the other transfers. When the four series of aggressiveness tests were finished all the data were submitted to an IBM program in which variance analysis, student t-tests, correlation analysis, etc., were carried out.

Data on temperature, relative humidity and precipitation for both regions were recorded during 1975 and 1976 (Table III and Figures 5 and 6) to help in the interpretation of the results. These data were supplied by meteorological stations and do not correspond to the exact moment when the aggressiveness tests were carried out. The observer also recorded the temperature at the moment of the test and the weights of the colonies on the day of the test as control of population size.

RESULTS

Behavioral characteristics (Aggressiveness)

Tables I and II show the results of aggressiveness tests done on colonies of Africanized bees in Ribeirão Preto, São Paulo State and in Recife, Pernambuco State. A total of 213 colonies were tested, of which 152 had transferred queens and 61 had untransferred queens (control). They were tested five times in each series of tests, corresponding to a total of 1065 aggressiveness tests carried out at both experimental stations. Table I shows the general results of the tests and Table II shows the statistical analysis.

Table I shows the results for two groups, the first consisting of offspring (workers) of transferred SP and PE queens, and the second representing the control (non-transferred queens). The result for the first group clearly shows the oscillation each time the queens were transferred from one region to the other, independently of the season of the year (see Fig. 1, 2 and 3). In general the data for the five behavioral characteristics showed an increase in aggressiveness when the queens were transferred to Recife and decrease in aggressiveness when they were transferred to Ribeirão Preto. The colonies were tested after the first queen transfer, but after this series of tests (Feb/76 in Recife, March-April in Ribeirão Preto) six queens from each lot were not transferred as would have normally been the case. Four to six months later these colonies were tested again in the same place (results in parentheses) and

le I – Results of four series of aggressiveness tests carried out from August 1975 to January 1977 on colonies of Africanized bees descen-
; from transferred and non-transferred (control) queens from Ribeirão Preto (SP-queens) and Recife (PE-queens). Data for behavorial
racteristics, hive weight and relative humidity on the day of the test and temperature at the moment of the test.

la I – Resultados de cuatro tests de agresividad llevados a cabo desde Agosto 1975 hasta Enero 1977 en colonias de abejas africanizadas
endientes de reinas transferidas y no transferidas (control) de Ribeirão Preto (reinas-SP) y Recife (reinas-PE). Datos de características
ductales, peso de la colmena y humedad relativa en el día del test y temperatura en el momento del test.

ERIES OF UEENS	NUMBER OF COLONIES	SITE OF TEST	DATE	BEHAVIORAL CHARACTERISTICS (AVERAGES) Nº 1 in sec.	Nº 2 in sec.	Nº 3 in meters.	Nº 4 in units/min.	Nº 5 units/min.	HIVE WEIGHT KG (AVERAGES)	TEMP (ºC) DURING TESTS (AVERAGES)	RELATIVE HUMIDITY % (AVERAGES)
P-QUEENS											
st Series	30	Ribeirão Preto	Sept/75	41.4	47.8	192.1	11.3	24.6	24.1	28.2	47.6
nd Series	26	Recife	Feb/76	33.6	44.3	171.4	17.6	24.2	26.9	28.3	61.7
rd Series	13 (6)	Recife	Aug/76	(24.2)	(31.8)	(255.8)	(16.4)	(59.9)	(31.5)	(25.7)	(67.2)
rd Series	7	Ribeirão Preto	July/76	56.6	59.6	18.0	0.2	0.6	25.7	24.5	54.7
th Series	6	Recife	Jan/77	26.9	29.5	267.1	23.5	118.2	34.2	32.2	-
Total	75										
E-QUEENS											
st Series	30	Recife	Aug/75	8.1	20.8	586.9	56.6	350.1	23.1	25.2	69.2
nd Series	27	Ribeirão Preto	March-Apr/76	37.7	45.6	112.5	12.3	14.3	21.4	27.2	64.7
rd Series	15 (6)	Ribeirão Preto	July/76	(51.3)	(58.8)	(2.3)	(1.7)	(0)	(27.0)	(24.2)	(50.1)
rd Series	9	Recife	Aug/76	34.3	39.9	163.8	18.9	16.0	33.0	26.0	59.5
th Series	5	Ribeirão Preto	Jan/77	44.0	53.8	44.4	4.6	1.9	30.0	25.9	73.1
Total	77										
P/PE-QUEENS											
st Series (SP)	10	Ribeirão Preto	Sept/75	35.9	44.0	264.5	13.2	21.0	23.6	30.0	50.6
st Series (PE)	10	Recife	Sept/75	8.0	23.1	541.1	41.7	166.3	21.4	25.0	67.9
nd Series (SP)	7	Ribeirão Preto	March-Apr/76	45.1	46.4	84.3	16.1	7.3	20.4	28.2	47.9
nd Series (PE)	7	Recife	Feb/76	20.5	33.6	265.7	34.0	75.0	25.8	26.7	69.3
rd Series (SP)	7	Ribeirão Preto	July/77	50.6	53.8	71.4	2.7	4.1	27.3	24.8	42.7
rd Series (PE)	7	Recife	Aug/76	25.7	37.1	208.7	18.9	22.0	34.1	26.0	66.6
th Series (SP)	7	Ribeirão Preto	Jan/77	42.0	56.6	49.8	6.2	2.2	30.4	27.8	60.4
th Series (PE)	6	Recife	Jan/77	13.1	15.5	407.6	48.3	218.5	34.5	31.6	-
Total	61										

avioral characters (aggressiveness)

Time until the first sting to the leather ball
Time for the colony to become aggressive
Distance that the bees follow the observer
Number of stings in the leather ball
Number of stings in the gloves of the observer

. – In the 3rd series of tests the numbers in parentheses
espond to the colonies whose queens stayed at the site after
first transfer and after 2nd series of aggressiveness tests.

Caracteristicas conductuales (agresividad)

1 – Tiempo transcurrido hasta antes de la primera picadura en la pelota de cuero
2 – Tiempo necesario para que la colonia sea agresiva
3 – Distancia que las abejas siguen al observador
4 – Numero de aguijones en la pelota de cuero
5 – Numero de aguijones en los guantes del observador

OBS. – En la 3ra serie de tests los numeros en parentesis corresponden a las colonias cuyas reinas permanecieron en su sitio después de la primera transferencia y después de la 2da serie de tests de agresividad.

the results showed that the colonies tested in Recife in August/76 had become more aggressive than the colonies tested in February/76. For example, for characteristic 1 (Fig. 1) «Time until the first sting to the leather ball», the average was 33.6 seconds in February/76 and 24.2 seconds in August/76, a time reduction representing an increase in aggressiveness. The same kind of response was observed for the other behavorial characteristics (Fig. 1 à 3).

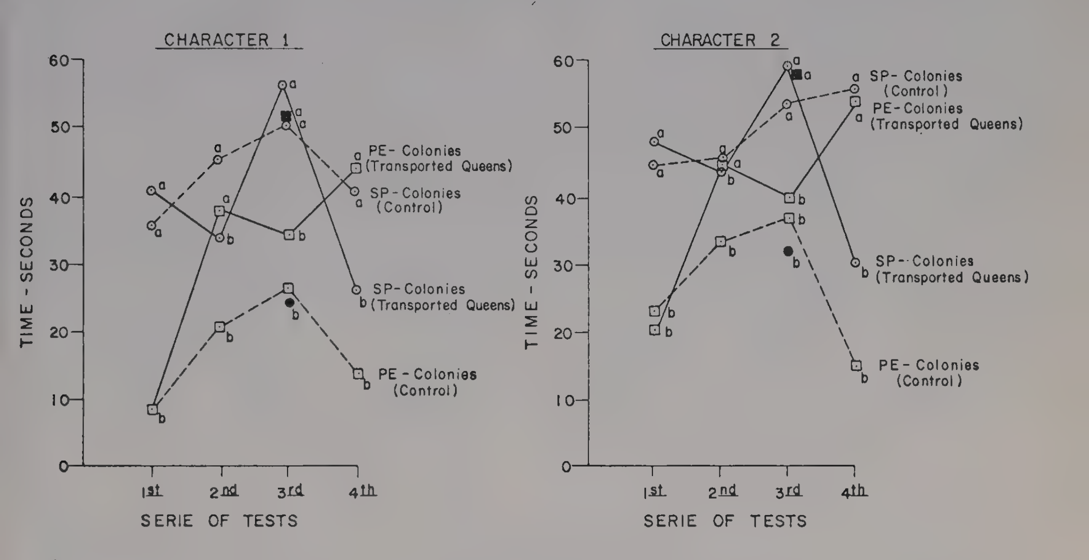


Fig. 1 – Results of aggressiveness tests carried out on Africanized bees descending from transferred and non-transferred (control) SP and PE queens. These graphs show the oscillation of response presented by the descendents of transferred queens after each queen transfer. The colonies whose queens remained at the site after the 2nd series of tests (in parenthesis in Table I) are shown in black.
Characteristic 1 = Time at which the first sting reaches the leather ball – Characteristic 2 = Time for the colony to become aggressive
Site of aggressiveness tests : a = Ribeirão Preto, SP – b = Recife, PE

Fig. 1 – Resultados de tests de agresividad llevados a cabo en abejas africanizadas descendientes de reinas SP y reinas PE transferidas y no transferidas. Estos gráficos muestran la oscilación de respuesta que presentan los descendientes de reinas transferidas después de la transferencia de cada reina. Las colonias cuyas reinas permanecieron en su lugar después de la 2da serie de tests (entre paréntesis en Tabla I) se muestran en negro.
Característica 1 = Tiempo en que el primer aguijón alcanza la pelota de cuero – Característica 2 = Tiempo que toma la colonia en llegar a ser agresiva
Lugar de los tests de agresividad : a = Ribeirão Preto, SP – b = Recife, PE

As to the PE queens, it can be seen that the colonies which were tested in Ribeirão Preto in March-April/76 became gentler in July/76. For example, see characteristic 1 in which the average increased from 37.7 seconds to 51.3 seconds. The response for the other characteristics was comparable.

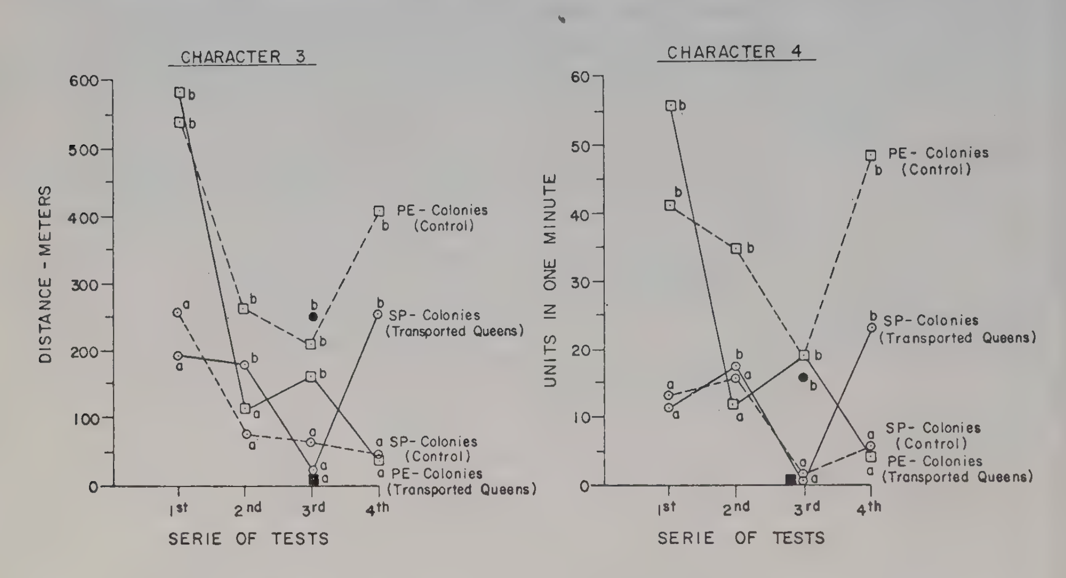


Fig. 2 – Results of aggressiveness tests carried out on Africanized bees descending from transferred and non-transferred (control) SP and PE queens. These graphs show the oscillation of response presented by the descendents of transferred queens after each queen transfer. The colonies whose queens remained at the site after the 2nd series of tests (in parentheses in Table I) are shown in black.
Characteristic 3 =Distance that the bees follow the observer – Characteristic 4 =Number of stings in the leather ball.
Site of aggressiveness tests : a =Ribeirão Preto, SP – b =Recife, PE

Fig. 2 – Resultados de tests de agresividad llevados a cabo en abejas africanizadas descendientes de reinas SP y reinas PE transferidas y no transferidas. Estos gráficos muestran la oscilación de respuesta que presentan los descendientes de reinas transferidas después de la transferencia de cada reina. Las colonias cuyas reinas permanecieron en su sitio después de la 2da serie de tests (entre paréntesis en Tabla I) se muestran en negro.
Característica 3 =Distancia que las abejas siguen al observador – Característica 4 =Número de aguijones en la pelota de cuero.
Lugar de los tests de agresividad : a =Ribeirão Preto, SP – b =Recife, PE

The second group of results in Table I (controls), is for 61 colonies with non-transferred queens only. These colonies were tested independently in each experimental station but always at the same time of the year, usually during the same month. The data for each series of five behavioral tests have been analyzed in pairs (SP and PE) in order to compare the results obtained in

Ribeirão Preto (for SP queens) and in Recife (for PE queens). The 20 pairs of data (SP and PE) for the controls always showed the same behavior, varying only in the degree of response. All of the data collected showed higher aggressiveness for the Recife Africanized bees when compared with the Africanized bees of Ribeirão Preto.

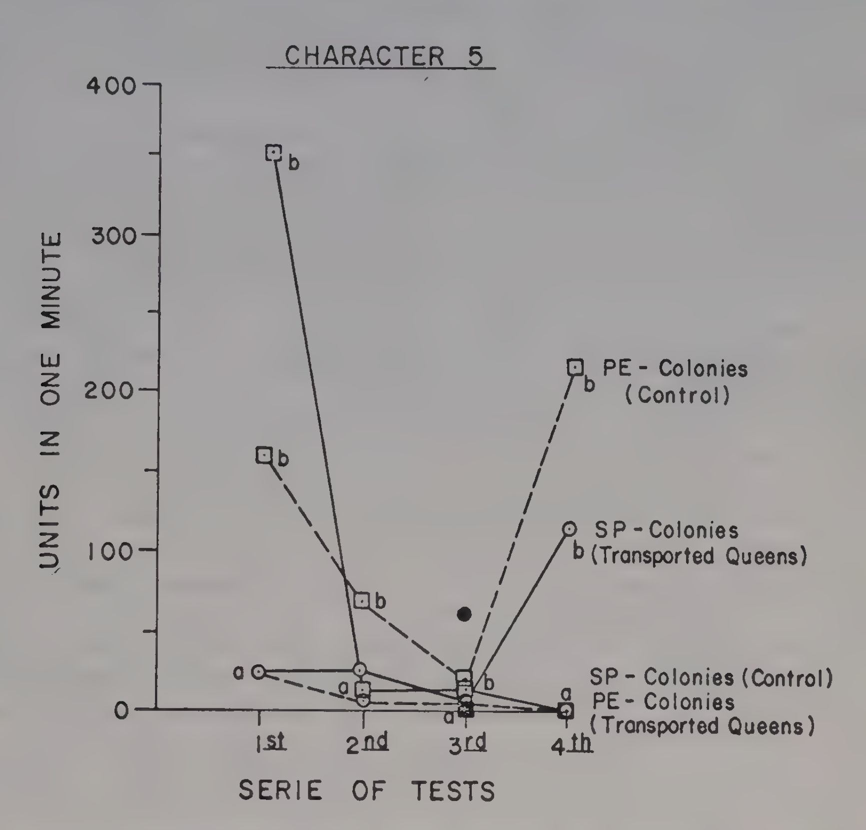


Fig. 3 – Results of aggressiveness tests carried out on Africanized bees descending from transferred and non-transferred (control) SP and PE queens. These graphs show the oscillation of response presented by the descendents of transferred queens after each queen transfer. The colonies whose queens remained at the site after the 2nd series of tests (in parentheses in Table I) are shown in black.
Characteristic 5 =Number of stings in the gloves of the observer
Site of aggressiveness tests : a =Ribeirão Preto, SP – b =Recife, PE

Fig. 3 – Resultados de tests de agresividad llevados a cabo en abejas africanizadas descendientes de reinas SP y reinas PE transferidas y no transferidas. Estos gráficos muestran la oscilación de respuesta que presentan los descendientes de reinas transferidas después de la transferencia de cada reina. Las colonias cuyas reinas permanecieron en su sitio después de la 2da serie de tests (entre paréntesis en Tabla I) se muestran en negro.
Característica 5 =Número de aguijones en los guantes del observador.
Lugar de los tests de agresividad : a =Ribeirão Preto, SP – b =Recife, PE

To focus on the results obtained in both regions and to make statistical comparisons, Table II was prepared from data in Table I. The results are presented in four groups according to the kind of comparisons made. The results of the t-tests are included in Table II and represented schematicaly in figure 4.

Groups 1 and 2 in Table II compare only data for transferred queens ; Group 3 compares only data for non-transferred queens (controls), and Group 4 compares the whole series of tests done in Ribeirão Preto with the whole series of tests done in Recife.

In Group 1 (transferred queens only) the aggressive behavior data for 75 SP-queens colonies obtained in Ribeirão Preto and in Recife were compared with the data for 77 PE-queens colonies also tested in both regions. This means that the pools of genes representative of the Africanized bees from each of the two regions were submitted to the climatic conditions of Ribeirão Preto and Recife during the whole experiment. Thus, in this group the average of the aggressive response for each characteristic analized represents the phenotype response of the Africanized bees from both Brazilian regions to the same climatic condition. As can be seen in Table I, first group, the bees responded differently each time they were moved from one region to the other. However, looking at Table II and Figure 4, it can be seen that the small differences observed between the averages of PE and SP colonies tested in both regions are not statistically significant. As an example, for characteristic number 2, «Time for the colony to become aggressive», the SP-queens workers had an average of 42.60 seconds and the PE-queens workers had an average of 43.78 seconds ($t = 0.14$ N.S.).

Thus, supposing that the Africanized bees from each region studied are hybrids which are being selected in nature for better adaptation to the climatic conditions of each region, the result for the first group in Table I and for group 1 in Table II lead us to postulate that natural selection for aggressiveness was surprisingly almost the same for both regions. We suppose also that the environmental conditions, especially the climatic conditions of each region (Ribeirão Preto and Recife), were mainly responsible for the different behavioral response recorded in Ribeirão Preto and in Recife, and for the similarity in behavioral responses when the «SP» and «PE» populations were submitted to the same environment of both regions.

In group 2 of Table II and Figure 4, which includes also transferred queens, the comparison was based on the site of the aggressiveness tests and the SP and PE colonies were included together in two lots. The data for 75 SP + PE colonies tested in Ribeirão Preto were compared with 77 SP + PE colonies tested in Recife, and the results showed different phenotypic (Aggressiveness) responses for characteristics 1, 2, 3 and 4. The apparent

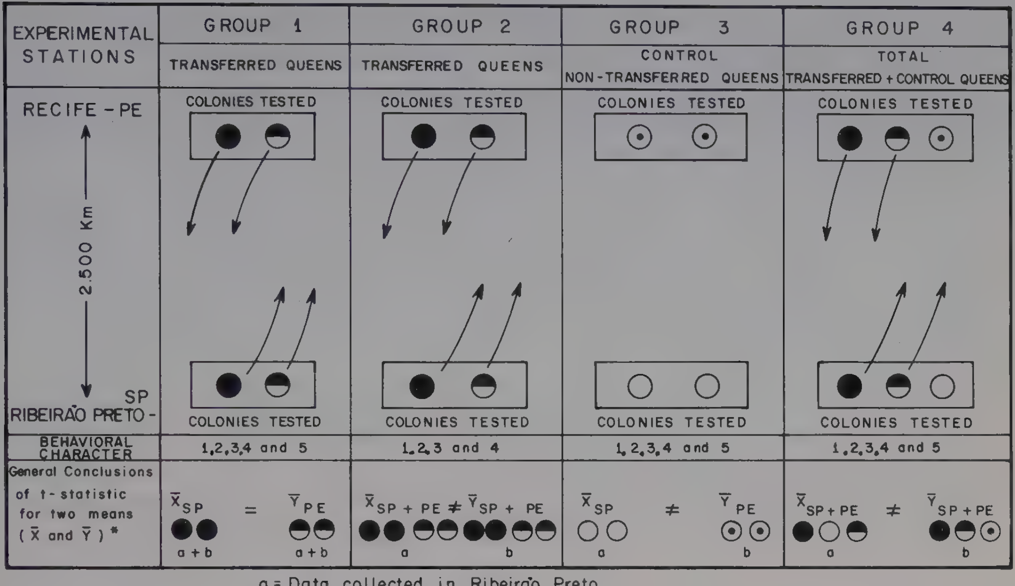


Fig. 4 – Schematic representation of four Groups of comparisons of data for aggressiveness tests on Africanized bees (see Table II) – Group 1 : Compares results for SP colonies (X_{SP}) tested in both regions (a + b) with results of PE-colonies (Y_{PE}) also tested in both regions – Group 2 : Compares results of SP + PE colonies tested in Ribeirão Preto : with results of SP + PE colonies tested in Recife – Group 3 : Compares results of the control colonies tested in their original places – Group 4 : Compares results of all colonies tested in Ribeirão Preto (transferred + control) with the results of all colonies tested in Recife (transferred + control).

Fig. 4 – Representación esquemática de cuatro grupos de comparaciones de datos para tests de agresividad en abejas africanizadas (ver Tabla II) – Groupo 1 : Compara resultados de colonias SP (X_{SP}) probadas en ambas regiones (a + b) con resultados de colonias PE (Y_{PE}) también probadas en ambas regiones – Grupo 2 : Compara resultados de colonias SP + PE probadas en Ribeirão Preto con resultados de colonias SP + PE probadas en Recife – Grupo 3 : Compara resultados de colonias control probadas en sus lugares de origen – Grupo 4 : Compara resultados de todas las colonias probadas en Ribeirão Preto (transferidas + control) con resultados de todas las colonias probadas en Recife (transferidas + control).

differences between the averages obtained for characteristic 5, «Number of stings in the gloves of the observer», were not statistically significant (t = -1.70). The results for group 2 show that the Africanized bees from both SP and PE transferred queens were much more aggressive in Recife than in Ribeirão Preto.

Table II – Results of student t-tests for four groups of data on agressiveness, tests carried out on colonies of Africanized bees descending from transferred (Groups 1 and 2), non-transferred queens (Control, Group 3) from Ribeirão Preto (SP-queens) and Recife (PE-queens), and total data (Group 4). Data for behavioral characteristics, hive weight on the day of the test and temperature at the moment of the test. NS = not significant – * = t-student statistically significant at a level of 5 %.

Tabla II – Resultados de tests-t de Student para cuatro grupos de comparaciones de datos sobre agresividad, llevados a cabo en colonias de abejas africanizadas descendientes de reinas transferidas (grupos 1 y 2), reinas non transferidas (grupo 3, control) de Ribeirão Preto (reinas-SP) y Recife (reinas-PE) y datos totales (grupo 4). Datos de características conductuales, peso de la colmena en el dia del test y temperatura en el momento del test. NS = significativo – * = test-t de Student estadisticamente significativos a nivel del 5 %.

GROUPS	QUEENS	Queens	Site of tests	Number of colonies	Date	Behavioral Characteristics (Averages)					Hive weight kg Averages	Temp. °C during tests Averages
						Nº 1 in sec.	Nº 2 in sec.	Nº 3 in meters	Nº 4 units/min.	Nº 5 units/min.		
1	TRANSFERRED	SP	Ribeirão Preto and Recife	75	Sept-75/Jan-77	36.54	42.60	180.88	13.80	45.50	28.48	27.78
		PE	Recife and Ribeirão Preto	77	Aug-75/Jan-77	35.08	43.78	181.98	18.82	76.46	26.90	25.70
						t=0.16 (NS)	t=-0.14 (NS)	t=-0.01 (NS)	t=-0.47 (NS)	t=-0.43 (NS)	t=0.55 (NS)	t=1.47 (NS)
2	TRANSFERRED	SP+PE	Ribeirão Preto	75	Sept-75/Jan-77	46.20	53.12	73.86	6.02	8.28	25.64	26.00
		SP+PE	Recife	77	Aug-75/Jan-77	25.42	33.26	289.00	26.60	113.68	29.74	27.48
						t=3.55*	t=3.98*	t=-2.53*	t=-2.58*	t=-1.70 (NS)	t=-1.63 (NS)	t=-0.98 (NS)
3	CONTROL	SP	Ribeirão Preto	31	Sept-75/Jan-77	43.40	50.20	117.50	9.53	8.65	25.43	27.70
		PE	Recife	30	Sept-75/Jan-77	16.83	27.33	355.78	35.73	120.45	28.95	27.55
						t=5.34*	t= 3.97*	t=-2.66*	t=-3.72*	t=-2.52*	t=-0.91 (NS)	t=0.09 (NS)
4	TOTAL	SP+PE	Ribeirão Preto	106	Sept-75/Jan-77	44.96	51.82	93.26	7.59	8.44	25.54	26.76
		SP+PE	Recife	107	Aug-75/Jan-77	21.60	30.62	318.68	30.66	116.69	29.39	27.51
						t=5.81*	t=5.71*	t=-3.79*	t=-4.29*	t=-2.90*	t=-1.85 (NS)	t=-0.68 (NS)

Behavioral characteristics (aggressiveness)

1 – Time until the first sting to the leather ball
2 – Time for the colony to become aggressive
3 – Distance that the bees follow the observer
4 – Number of stings in the leather ball
5 – Number of stings in the gloves of the observer

Caracteristicas conductales (agresividad)

1 – Tiempo transcurrido hasta antes de la primera picadura en la pelota de cuero
2 – Tiempo necessario para que la colonia sea agresiva
3 – Distancia que las abejas siguen al observador
4 – Numero de aguijones en la pelota de cuero
5 – Numero de aguijones en los guantes del observador

Group 3 in Table II (see Fig. 4) consists of data for non-transferred queens, the control group. The averages for the 31 SP-colonies and 30 PE-colonies correspond to the means of the four series of tests (control) presented in Table I. The Africanized bees from each region were tested in their original environment and the results were compared. As an example, characteristic 1, «Time until the first sting to the leather ball», was 43.40 seconds in Ribeirão Preto and 16.83 seconds in Recife (t = 5.34, statistically significant at the 5 % level). For characteristic 3 «Distance that the bees follow the

observer», the Ribeirão Preto Africanized bees averaged 117.50 meters and the Recife bees averaged 355.78 meters (t = - 2.66, statistically significant at the 5 % level). For characteristic 5 «Number of stings in the gloves of the observer» the average in Recife (120.45 units in one minute) was 14 times higher than in Ribeirão Preto (8.65 units in one minute) and the difference was statistically significant at the 5 % level (t = - 2.52). The results for these control colonies show that the Recife Africanized bees were much more aggressive than the Ribeirão Preto bees.

Group 4 in Table II consists of data for 213 colonies of Africanized bees from both Brazilian regions, with 152 colonies descending from transferred queens and 61 from the controls. The data were grouped into two lots, according to the place where they were obtained. The data for 106 SP + PE colonies tested in Ribeirão Preto were compared with the data for 107 SP + PE colonies tested in Recife. By looking at the results of this group it can be said that, in general, the Africanized bees descending from SP and PE queens, whether transferred or not, when tested in Recife, were much more aggressive than when tested in Ribeirão Preto. All the t-tests were statiscally significant at the 5 % level.

The results for the four groups of comparisons presented in Table II and Figure 4 led us to the conclusion that the Africanized bees from both Brazilian regions respond identically when in the same environment (climatic conditions). We concluded that the Africanized bees are much more aggressive in Recife than in Ribeirão Preto. The Africanized bees of both regions, when transported from one region to the other, respond with higher aggressivity in the Northeast of Brazil and lower aggressivity in the Southeast of Brazil because of the different climatic condition of these regions. The aggressive behavior of the populations of Africanized bees in each region was much more influenced by external factors (climatic conditions) than by their genotypic compositions.

Considerations on the climatic conditions of Ribeirao Preto (SP) and Recife (PE)

Temperature (see Table III and Fig. 5) : the yearly average temperature in Ribeirão Preto was 20.85° C in 1975 and 20.65° C in 1976. The average maximum was 31.8°C in 1975 and 29.5°C in 1976 and the minimum average was 9.9° C in 1975 and 11.8° C in 1976. The variability rate (maximum-minimum) was 22°C in 1975 and 18°C in 1976. In Recife the yearly average temperature was 26.40° C in 1975 and 25.05° C in 1976. The average maximum was 32.7° C and 31.2° C in 1975 and 1976, respectively. The minimum

Table III – Climatic data (temperature, relative humidity and precipitation) for the regions of Ribeirão Preto (SP) and Recife (Tapacurá) (PE), where aggressiveness tests with Africanized bees were carried out. Data were collected in 1975 and 1976 by the meteorological stations* in both regions.

Tabla III – Datos climáticos (temperatura, humedad relativa y precipitación) para las regiones de Ribeirão Preto (SP) y Recife (Tapacurá) (PE), donde se realizaron los testes de agresividad con abejas africanizadas. Los datos fueron colectados en 1975 y 1976 por las estaciones meteorológicas* de ambas regiones.

Site	Year	Temperature (averages) °C			Relative humidity (averages) %			Precipitation MM		
		Max.	Min.	Mean	Max.	Min.	Mean	Total	Max. Occur.	Min. Occur.
Ribeirão Preto (SP)	1975	31.8	9.9	20.85	65.5	24.7	45.1	1,759.5	Nov.	May
Altitude : 621 meters Latitude : 21° 11' S Longitude : 47° 43, W/GR	1976	29.5	11.8	20.65	68.1	44.7	56.2	1,523.6	Febr.	April
Recife (Tapacurá) (PE)	1975	32.7	20.1	26.40	77.0	54.0	65.5	1,524.4	July	Oct.
Altitude : 120 meters Latitude : 8° 9' S Longitude : 35° 6'W/GR	1976	31.2	18.9	25.05	72.0	59.0	65.5	1,090.8	March	Sept.

OBS. Distance from Ribeirão Preto to Recife (Tapacurá) : 2.500 km

* Instituto de Pesquisas Agronômicas – Setor de climatología Agricola – Recife-PE
Secretaria da Agricultura do Estado de São Paulo – Inst. Agronômico – Secção Climatologia Agrícola

average was 20.1° C and 18.9° C in 1975 and 1976, respectively. The variability rate was 12° C in both 1975 and 1976.

These results show that the yearly average temperature is at least 5° higher in Recife, and that the temperature oscillation in Ribeirão Preto is about twice the oscillation in Recife. The honeybees suffer a higher temperature oscillation in Ribeirão Preto than in Recife where the temperature is more stable throughout the year and where there is practically no winter season.

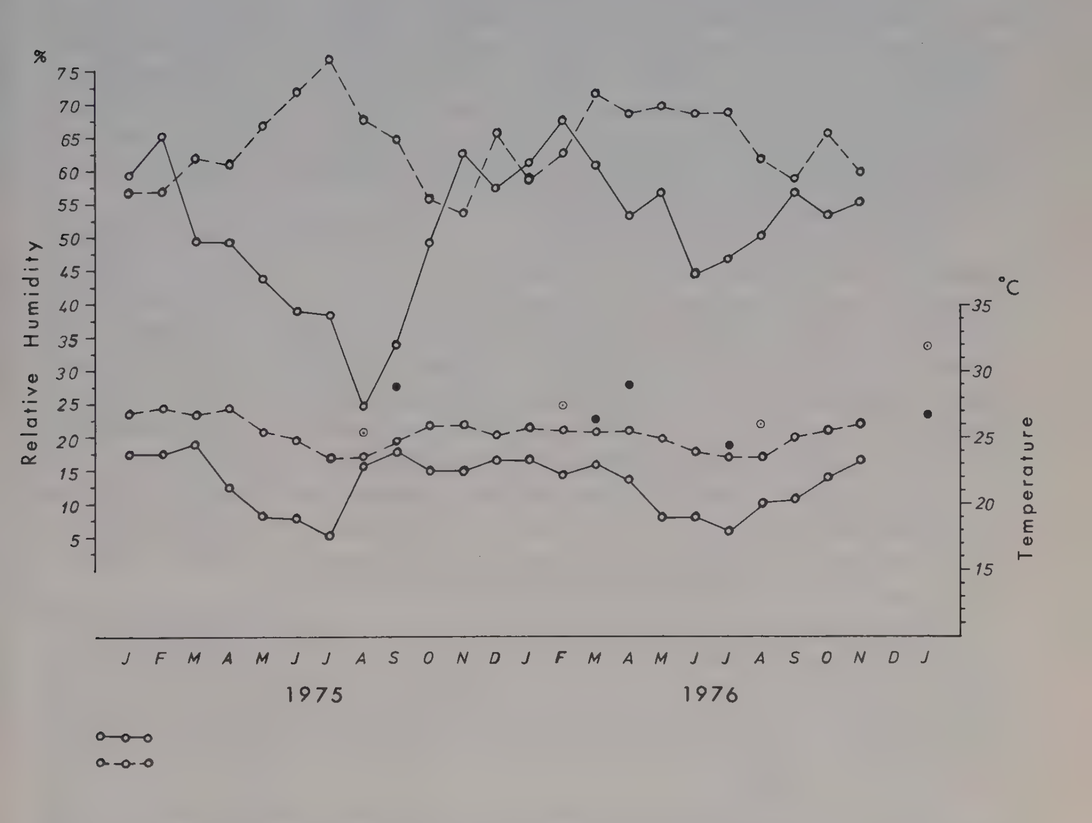


Fig. 5 — Monthly climatic date for temperature and relative humidity in Ribeirão Preto (SP) and Recife (PE) during 1975 and 1976. The average temperature at the times of the aggressiveness tests is shown by black (Ribeirão Preto) and dotted (Recife) circles.

Fig. 5 — Datos climáticos mensuales de temperatura y humedad relativa en Ribeirão Preto (SP) (líneas continuas) y Recife (PE) (líneas entrecortadas) durante 1975 y 1976. Las temperaturas medias al momento de los tests de agresividad se indican por círculos negros (Ribeirão Preto) y círculos punteados (Recife).

Tables I and II show that there was no difference between the average temperature recorded during the aggressiveness tests. However, it must be mentioned that 90 % of the tests were carried out between 2 PM and 4 PM in both experimental stations and this is the warmest period of the day. This is the reason why the mean temperatures recorded in Tables I and II are higher than the averages recorded in Table III and Figure 5, which correspond to the yearly average temperatures based on data collected daily by both regional meteorological stations.

The correlation analysis presented later was made by considering only the temperatures recorded by the experimenter at the moment of the aggressiveness test and not the data collected by the meteorological stations. Thus, it is possible that the aggressive responses showed by the bees are related not only to the influence of temperature on that particular day or at the moment of test but also by the temperature of one, two, or more days before the test. This analysis was not done and the correlation analysis of the temperature with other variables will be discussed later.

Humidity (see Table III and Fig. 5) : the relative humidity in Recife (Tapacurá) was higher than in Ribeirão Preto in both 1975 and 1976. In Ribeirão Preto the mean relative humidity in 1975 and 1976 was 45.1 % and 56.2 %, respectively, and in Recife 65.6 % in both years. However, the oscillation of the relative humidity was higher in Ribeirão Preto. The minimum in Ribeirão Preto to was 24.7 % in 1975 and 44.7 % in 1976, and in Recife 54.0 % and 59.0 % in 1975 and 1976, respectively. The Recife region has a higher and more stable relative humidity than Ribeirão Preto.

The relative humidity data for both regions were obtained by the meteorological stations and not by the experimenter at the moment of the aggressiveness tests. Thus, the data used for the correlation analysis that will be discussed later correspond to the mean of the day.

Precipitation (see Table III and Fig. 6) : in the years 1975 and 1976 the precipitation in Ribeirão Preto (1759 mm and 1523 mm) was higher than in Recife (1524 mm and 1090 mm). The rainy season in Recife is the March-August period, in Ribeirão Preto the November-March period. Figure 6 shows that the precipitation in Ribeirão Preto is better distributed throughout the year than in Recife.

In July 1975 there was excessive precipitation in Recife which caused catastrophic flood. In 1976 the rainy season was normal, but in 1977 the rainy season again caused a severe flood in Recife although less than in 1975. Despite the fact that the yearly precipitation in Recife is lower than in Ribeirão Preto, the relative humidity is higher in Recife due the fact that Recife (Tapacura) is about 120 meters above sea level and Ribeirão Preto is 621 meters above sea level.

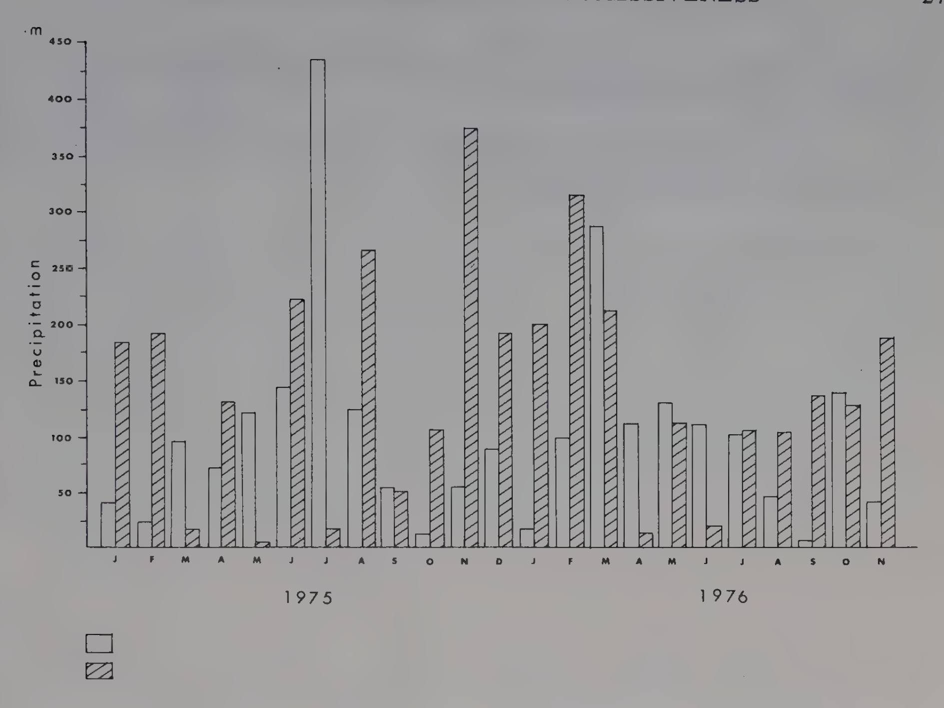


Fig. 6 – Monthy precipitation in Ribeirao Preto (SP) white and Recife (PE) (cross hatched) during 1975 and 1976.

Fig. 6 – Precipitación mensual en Ribeirão Preto (SP) (blanco) y Recife (PE) (achurado) durante 1975 y 1976.

Considerations on the weight of the colonies

In order to check the size of the honeybee population of each colony used which had only one super, bottom and cover, the colonies were weighed the day before each aggressiveness test. At the beginning of the experiment all colonies had about the same bee population and the hives had about the same weight. At the end of the experiment the averages of the SP-colonies did not differ statistically from the averages of the PE-colonies. The results are shown in Table II. The t-student tests were not statistically significant in the four groups comparisons. Mean weight of the hives in Ribeirão Preto was 25.54 kg and in Recife 29.39 kg (t = 1.85, N.S.). However this record must not be considered as representative of productivity because the hives had no honey supers, no honey flow control, and most were submitted to a constant program of queen substitution after each transfer between the two experimental stations.

Table IV – Correlation analysis (total data) between 5 behavioral characteristics (X_1, X_2, X_3, X_4 and X_8), 2 climatic variables (temperature X_5 and relative humidity X_7) and hive weight (X_6). Data for Africanized bees from Ribeirao Preto and Recife.

Tabla IV – Análisis de correlación (datos totales) entre 5 características conductuales (X_1, X_2, X_3, X_4 and X_8), 2 variables climáticas (temperatura, X_5 y humedad relativa, X_7) y peso de la colmena (X_6). Datos para abejas africanizadas de Ribeirão Preto y Recife.

	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
X_1		- 0.88*	- 0.83*	- 0.50*	- 0.08 NS	- 0.01 NS	- 0.20*	0.91*
X_2			0.84*	0.70*	0.05 NS	- 0.05 NS	0.14 NS	- 0.88*
X_3				0.68*	0.01 NS	- 0.04 NS	0.20*	- 0.81*
X_4					- 0.07 NS	- 0.04 NS	0.15 NS	- 0.54*
X_5						- 0.06 NS	- 0.41*	- 0.07 NS
X_6							- 0.05 NS	0.02 NS
X_7								- 0.17*
X_8								

Variables : X_1 : Time until the first sting to the leather ball – X_2 : Distance that the bees follow the observer – X_3 : Number of stings in the leather ball – X_4 : Number of stings in the gloves of the observer – X_5 : Temperature at the moment of the test – X_6 : Weight of each colony on the day of the test – X_7 : Relative humidity in the region – X_8 : Time for the colony to become aggressive.
N =135 – * : Significant at 5 % level – r = 0.17 – NS = Not significant.

Variables : X_1 : Tiempo transcurrido hasta antes de la primera picadura en la pelota de cuero – X_2 : Distancia que las abejas siguen al observador – X_3 : Número de aguijones en la pelota de cuero – X_4 : Número de aguijones en los guantes del observador – X_5 : Temperatura al momento del test – X_6 : Peso de cada colonia en el día del test – X_7 : Humedad relativa en la región – X_8 : Tiempo necesario para que la colonia sea agresiva.
N =135 – * : Significativo a nivel del 5 % – r = 0.17 – NS = No significativo.

Correlation analysis among the five behavioral characteristics : temperature, relative humidity and weight of the hives

A Pearson product-moment correlation analysis was performed on the data collected in both experimental stations in 1975 and 1976. The analysis was carried out in two ways : with the total data (Table IV), and with the data of Ribeirão Preto and Recife processed separately (Table V). The eight variables were coded as follow :

X_1 : Time until the first sting to the leather ball.
X_2 : Distance that the bees follow the observer.
X_3 : Number of stings in the leather ball.
X_4 : Number of stings in the gloves of the observer.

X_5 : Temperature at the moment of the test.
X_6 : Weight of each colony on the day of the test.
X_7 : Relative humidity in the region.
X_8 : Time for the colony to become aggressive.

Behavorial variables (X_1, X_2, X_3, X_4 and X_8). The correlation analysis presented in Tables IV and V shows that there was a significant correlation among all the variables related to aggressive behavior, in both types of analysis, i.e. total data and data separated according to region. For instance, in Table IV the characteristic, «Time until the first sting to the leather ball», showed a negative correlation with the characteristics, «Distance that the bees follow the observer» (r = - 0.88), «Number of stings in the leather ball» (r = - 0.83), and «Number of stings in the gloves of the observer» (r = - 0.50) and a positive correlation with the «Time for the colony to become aggressive» (r = 0.91).

The same kind of relationship among the behavioral characteristics was observed separately (Table V). The only exception was for the correlation between the «Time until the first sting to the leather ball» and «Number of stings in the leather ball», but the data collected in Ribeirão Preto showed a negative correlation (r = - 0.82) which means that, the shorter the time for the first sting to occur, the higher the number of stings in the ball. However, in Recife the correlation was positive (r = 0.80), which is a curious fact without a clear explanation because, when it loses its sting the bee releases an alarm substance which attracts new bees to that site.

From the correlation analysis (Tables IV and V) we can conclude that, in general, there was good relationship among the 5 variables related to aggressive behavior, in agreement with the observations by Stort (Gonçalves and Stort, 1977).

Temperature (variable X_5). The only significant result observed in Table IV (total data) was the correlation between temperature at the moment of the tests and relative humidity on the day of the test (t = - 0.41). The other variables showed no significant correlation with temperature. The data collected in Recife and Ribeirão Preto showed other significant correlations among the variables when they were analyzed separately, as can be seen in Table V.

In Ribeirão Preto, the temperature, which is lower than in Recife (see Table III), showed a positive and significant correlation with the «Time until the first sting to the leather ball» (r = 0.27), with the «Distance that the bees follow the observer» (r = 0.33), with the «Number of stings in the leather ball» (r = 0.25), with the «Number of stings in the gloves of the

Table V – Correlation analysis between 5 behavioral characteristics (X_1, X_2, X_3, X_4 and X_8), 2 climatic variables (temperature X_5 and relative humidity X_7) and hive weight (X_6). Data for Africanized bees from Ribeirão Preto (A) and Recife (B).

Tabla V – Analisis de correlación entre 5 características conductuales (X_1, X_2, X_3, X_4 and X_8), 2 variables climáticas (temperatura, X_5 y humedad relativa, X_7) y peso de la colmena (X_6). Datos para abejas africanizadas de Ribeirão Preto (A) y Recife (B).

		X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
X_1	A		- 0.86*	- 0.82*	- 0.70*	- 0.27*	- 0.09 NS	- 0.01 NS	0.93*
	B		- 087*	0.80*	- 049*	0.23*	0.25*	- 0.21 NS	0.88*
X_2	A			0.74*	0.78*	0.33*	- 0.07 NS	- 0.15 NS	- 0.86*
	B			0.84*	0.72*	- 0.29*	- 0.34*	0.18 NS	- 0.86*
X_3	A				0.84*	0.25*	0.01 NS	- 0.07 NS	- 0.84*
	B				0.67*	- 0.30*	- 0.33*	0.27*	- 0.75*
X_4	A					0.30*	0.07 NS	- 0.15 NS	- 0.72*
	B					- 0.27*	- 0.25*	0.13 NS	- 0.53*
X_5	A						- 0.10 NS	- 0.48*	- 0.29*
	B						0.02 NS	- 0.27*	0.26*
X_6	A							- 0.25*	0.10 NS
	B							- 0.17 NS	0.22*
X_7	A								- 0.01 NS
	B								- 0.15 NS
X_8	A								
	B								

Variables : idem to Table IV.
A : In Ribeirão Preto, N = 61 – B : In Recife, N = 74 – * Significant at 5 % level – NS = Not significant.

Variables : idem Tabla IV.
A : En Ribeirão Preto, N = 61 – B : En Recife, N = 74 – * Significativo a nivel del 5 % – NS = No significativo.

observer» (r = 0.30), and negative correlation with the «Relative Humidity» (r = - 0.48) and with «Time for the colony to become aggressive». These results mean that, in Ribeirão Preto, the higher the temperature the higher the aggressiveness. Stort (1971) did not find a correlation between temperature and aggressive behavior in data collected in Ribeirão Preto with Italian and Africanized bees.

In Recife, where the temperature is more stable and higher than in Ribeirão Preto, the relationship between the temperature and the other variables analyzed was different where compared with the results observed in Ribeirão Preto.

The temperature was positively correlated with only two characteristics in Recife : «Time until the first sting to the leather ball» (r = 0.23) and «Time for the colony to become aggressive» (r = 0.26). For this last characteristics (X_8) the result was opposite to that in Ribeirão Preto where the correlation was negative (- 0.29). This means that in Ribeirão Preto the aggressiveness of the Africanized bees (character X_8) increases with increase of temperature and in Recife the aggressiveness diminishes with increase of temperature. The temperature presented a negative and significant correlation with the following characteristics : «Distance that the bees follow the observer» (r = - 0.29), «Number of stings in the leather ball» (r = - 0.30), and «Number of stings in the gloves of the observer» (r = -0.27). This means that in Recife the aggressivenes of the Africanized bees does not increase with the increase in temperature as observed in Ribeirão Preto.

It is interesting to note the difference in relationship between temperature and aggressive behavior in these two regions of Brazil. The results were surprising, which leads us to think that other variables must be interacting with this behavior. However, it must be remembered that, on the average, the temperature in Recife is at least 5°C higher than in Ribeirão Preto and that the yearly temperature oscillation in Recife is low compared to that observed in Ribeirão Preto. The results of the Aggressiveness tests presented in Tables I and II showed that the Africanized bees were much more aggresive in Recife than in Ribeirão Preto. The statistical tests carried out with the data for the four comparison groups presented in Table II led to the conclusion that the factors mostly responsible for the higher aggressiveness of the Recife Africanized bees were climatic and not genetic. These results confirm experimentally the hypothesis of Schua (1952), Rothenbuhler (1974), Warnke (1977) and the field observations of Gebreyesus (1976).

Relative humidity (variable X_7). The relative humidity on the day of the test showed a negative correlation with temperature at the moment of the test (r = - 0.41) (Table IV). The data for Ribeirão Preto (r = - 0.48) and Recife (r = - 0.27) (see Table V) gave the same results. The relationship between the

humidity and the other variables was not the same in both regions. It must be remembered that the relative humidity is higher in Recife (Tapacurá) than in Ribeirão Preto (see Table III and Fig. 5). Correlation analysis of total data showed positive correlation with only one characteristic, «Number of stings in the leather ball» (r = 0.20). There were negative correlations with the following characteristics : «Time until the first sting to the leather ball» (r = - 0.20) and «Time for the colony to become aggressive» (r = - 0.17). This means that the higher the relative humidity, the higher the aggressiveness of the bees. The other results were not statistically significant.

In Ribeirão Preto, the relative humidity (45.1 % in 1975 and 56.2 in 1976, Table III) had no influence on the aggressiveness of Africanized bees, according to the results for variables X_1, X_2, X_3, X_4 and X_8 presented in Table V, all of which were not statistically significant.

In Recife the relative humididy (65.5 % in 1975 and 1976, Table III) had a positive correlation with the characteristic «Number of stings in the leather ball» (r = 0.27). Correlations with other variables related to aggressiveness were not statistically significant.

It appears that the data for Ribeirão Preto and Recife, when analyzed separately, were not sufficient to provide a good analysis. The total data permitted a better analysis, and the results seem to agree with those of the aggressiveness tests, because the Africanized bees in Recife, where the humidity is higher, showed a much higher aggressiveness than those in Ribeirão Preto. This research is not conclusive as to the effect of temperature and humidity on the aggressive behavior of Africanized bees, but the results support the hypothesis that the aggressive behavior of Africanized bees is much influenced by relative humidity in Recife and more influenced by temperature in Ribeirão Preto.

Weight of the hives (variable X_6). The correlation analysis with the total data showed no significant relationship between this variable and the other variables sutied (Table IV).

The data collected in Ribeirão Preto showed only one significant result, the negative correlation between «Relative Humidity» and «Weight of the hive» (r = - 0.25). In Recife there was a positive correlation between «Weight of the hive» and «Time until the first sting to the leather ball» (r = 0.25), and the «Time for the colony to become aggressive» (r = 0.22). Comparisons of the averages for the hives from Ribeirão Preto and Recife showed no significant differences (see Table II). The results for both correlation analyses (Total data and data analyzed separately) were not sufficient to give a conclusive answer about the influence of the weight of the hive on aggressive behavior ; on the other hand, the variable «Weight of the hive»

was not used to study its influence on aggressive behavior but only as a control for colony size, as previously mentioned.

CONCLUSIONS

The general nature of aggressive behavior in honeybees, which can be considered as a phenotype, is the product of interaction between genetic composition (Genotype) and environmental factors. In many cases it is difficult to decide which of these two components (Genotype and Environment) is more important. Genetic behavior analysis of whole colonies requires a worker homogeneity which can be obtained, for example, by backcrossing a drone from a F_1 queen with a virgin queen of the parental inbred line (Rothenbühler, 1960). Some responses are caused by internal or external factors ; climatic conditions, for example, can be external factors influencing bee aggressiveness (Schua, 1952 ; Lecomte, 1963 ; Rothenbuhler, 1964 ; Warnke, 1976, etc.). It must also be pointed out that the chain reaction observed in bee stinging is defensive behavior rather than a form of aggression. This means that the honeybees react or respond in a definite pattern to specific stimuli.

In conclusion it can be said that the aggressive behavior of Africanized bee populations in both regions studied was much more influenced by external factors (climatic conditions) than by the bees'genotypic composition. Our results confirm experimentally the hypothesis of Schua (1952), Rothenbuhler (1974) and Warnke (1977), who pointed out the importance of climatic conditions on the aggressive behavior of bees. This research also confirms that the genes for aggressive behavior obviously do not function alone but interact with environmental factors to produce the final behavioral phenotype.

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1 M.M. BRANDEBURGO – Dept. de Genetica – F.M.R.P. – USP – Ribeirão Preto, S.P., Brazil.
2 L.S. GONÇALVES – Fac. Fil. C.L. de Ribeirão Preto – USP – Ribeirão Preto, S.P., Brazil.
3 W.E. KERR – Dept. de Biologia – Univ. Fed. Maranhão – Sao Luis, M.A., Brazil.

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